Duff Consumption and Southern Pine Mortality

Project: JFSP 01-1-3-11

J. Kevin Hiers[1,2]
Doria R. Gordon[2]
Robert J. Mitchell[3]
Joseph J. O'Brien[4]

[1]Eglin Air Force Base
[2]The Nature Conservancy
[3]J. W. Jones Ecological Research Station
[4]USDA Forest Service, SRS-4104

The Nature Conservancy
Thomasville, GA
September 2, 2005

TABLE OF CONTENTS

EXECUTIVE SUMMARY

Smoldering duff, accumulated organic matter, following burning in fire-excluded systems in the SE United States, is increasing problematic for restoration, conservation, and reduced wildfire risk reasons. Prolonged smoke generation and wildfire risk accompany this smoldering, which can support new surface fire ignition long after the fire is assumed extinguished. In addition, mature trees often now die after fire. This mortality may be delayed for two or more years post-fire. Because mature longleaf pine trees are now rare across the southeastern coastal plain, mortality of even a small percentage of the few large pines remaining is counter to management goals. This study was comprised of 6 major tasks: (1) determine threshold moisture conditions for duff smoldering; (2) develop prescription guidelines to safely burn when duff is present while avoiding consumption thresholds; (3) describe stand structure and forest floor characteristics associated with consumption, (4) track foliar and root dynamics following consumption of duff, (5) survey mortality associated with levels of consumption, and (6) explore mechanistic relationships between consumption and individual tree mortality. The research addressed Issue 3 (evaluate and compare fuels treatment practices and techniques) and Tasks 1 and 3 of the spring 2001 Joint Fire Science Program request for proposals.

Cones and other 10 and 100 hr fuels that accumulate beneath trees generate sufficient heat to ignite the duff, which can then smolder long after the surface fire has been extinguished and result in temperatures lethal to living tissues (> 60^{o} C) at 20 cm depth in mineral soil. Neither smoldering nor observed tree response was predicted by the fire effects modeling software, FOFEM. Duff moisture significantly influences the probability of ignition. Other fire impacts, like canopy scorch, only increased the probability of tree mortality under dry duff conditions. Our data, from experimental and validation fires, suggest that if duff moisture is above 90% of the volumetric water content (based on dry weights) on the day of the burn, smoldering fires are less likely to occur. During months of high evapotranspiration, results suggest that >1.5 inches or 1 inch of rain combined with >12 hours duration of rainfall should be sufficient to preclude duff fires during normal climatic conditions. Data on ignition characteristics under different duff moisture levels have now been included in the fuel model, Consume version 3.0, to allow refinement of burn prescriptions in pine systems with high duff accumulation in the forest floor.

We also experimentally examined the mechanism by which smoldering duff fires increase longleaf pine tree stress, and the probability of tree mortality. As indicators of stress, changes in stem radial growth would represent an aggregate of current and preceding year's stresses, while carbohydrate supplies are metrics of current tree stress. Radial stem growth (% change from pre-burn ring radius) significantly decreased with increased heating duration > 60º C within the top 5 cm and 10 cm of mineral soil. Latewood growth was more sensitive to this heating than was earlywood. Additionally, heating > 60º C at 5 cm depth in the mineral soil caused coarse (but not fine) root carbohydrate loss ($p<0.01$), explaining 59% of the variation in post-burn changes in coarse root carbohydrates. These carbohydrates losses strongly support the role of coarse root mortality from mineral soil heating as the primary cause of post-fire stress and potentially mortality in old growth trees.

INTRODUCTION

In the southeastern U.S., fire is an essential process for maintaining ecosystems and reducing wildfire risks in the urban interface. Managers are increasingly expected to use fire as a landscape-level fuel treatment to improve ecosystem health and reduce the likelihood of catastrophic fires. Decades of fire-exclusion in many forests throughout the southeast have resulted in significant accumulation of organic matter (duff) on the forest floor. More than 50% of the extant longleaf pine stands have not received frequent fire (Varner and Kush 2001, Outcalt 2000). The reintroduction of fire into these forests has proven problematic on two fronts. Following prescribed fire in stands where duff is consumed, extensive delayed mortality of longleaf pines can result. All too many of the few remaining old-growth stands in the southeast are also in this condition, and fire-induced mortality of especially older trees is a great conservation concern. Moreover, rapidly expanding suburban growth into these fire-excluded stands has created significant hazards from fuel loading. Fuel reduction burns in these stands that result in smoldering combustion within the duff layer increase the potential hazards and nuisance of residual smoke. Flare-ups and reburn of these stands from needle drop re-ignited by smoldering duff are also wildfire risks. An environmentally aware public has required managers to improve their decision-making processes and use tradeoff models and various regulatory requirements to better assess land use decisions. Fuel consumption is the key variable in the modeling of these fire effects. Thus, applying this understanding towards identifying both threshold conditions under which duff smolders and the consequences of duff consumption to tree mortality is vital to southeastern fire managers and successful restoration of long-unburned southern pine stands throughout the South.

Although this research is regional in scope, comparatively little research has been done in southeastern fuel beds, particularly in long-duration fuels. The rapidly expanding urban interface in this region and dramatically increased number of questions/complaints fielded by state fire protection agencies since the 1998 Florida wildfires emphasize the importance of this issue to both the public and fire managers in the southeast. This situation is also common in other regions of the country where deep organic layers have accumulated around the base of large pine trees, creating a potential for mortality when fire is applied (e.g., Swezy and Agee 1991). Finally, linkages with other proposals that are broader in geographic scope and the incorporation of results into consumption modeling provide a larger context for application of these results. For example, the field data we collected in the course of this study allowed us to empirically validate previously developed fuel consumption models for their accuracy, and refine conditions necessary for duff consumption.

Although some research on consumption models for smoldering fuels exists (Ottmar et al 1998), only a small portion of that effort has been directed toward characterizing long duration fuel consumption from deep concentrations of organic material such as duff. Further, while managers across the southeastern U.S. have anecdotal reports of high overstory tree mortality from prescribed fire in areas that have had low fire frequency, little research has identified the cause or frequency of that mortality (Swezy and Agee 1991, Doren et al. 1993, Menges and Deyrup 2001). Hypotheses about the mechanisms resulting in tree mortality generally involve direct effects of fire, such as root damage, girdling, leaf scorch, and meristem damage, and indirect effects, such as *Ips* or *Platypus* spp. beetle damage following fire-induced stress. Degree of tree stress may be indicated by changes in carbon balance, reflected by stem or root tissue carbohydrate levels. The extent that older trees may be disproportionately influenced may be due to greater duff accumulation in larger older trees, but may also be exacerbated by less resilience to carbon drain (i.e. older trees may be less able to direct C to replace and repair roots damaged in the fire, Yoder et al. 1994). Direct or indirect mortality appears likely to be linked to fire intensity and duration, particularly in the duff layer. For example, duff fires in mature longleaf pines in Alabama resulted in mortality of 91% of all trees > 38 cm dbh (Kush and Varner 1999). However, insufficient research has focused on the patterns of this relationship between duff volume and condition (i.e., moisture levels), carbon balance, and pine mortality. This project used experimentation to examine and differentiate among the several hypothesized mechanisms of mortality.

This research involved collaboration among both Forest Service and independent researchers who are experts in southeastern pine fuels and fire ecology. Specific expertise in theoretical and empirical fuel consumption modeling (Sandberg 1980, Sandberg and Ottmar 1983, Ottmar and others 1993) and prescribed fire management and training (Wade and Johansen. 1986, Wade and Lunsford 1989, The Nature Conservancy) and conservation (The Nature Conservancy) complemented the forest science. Through this cooperative effort, we have had a unique opportunity to assess overstory mortality under a range of duff moisture contents and to apply that knowledge to conservation of southern pine resources and hazardous fuel reduction throughout the southeast. This report is an integration of the individual contributions of each of the institutions funded through the U.S. Forest Service on this Joint Fire Science Program grant.

OBJECTIVES

The primary objectives of this project were to:

1) Determine threshold moisture conditions that initiate and maintain smoldering combustion within the forest floor of longleaf pine stands and to document the consequences of this combustion for overstory tree mortality.
2) Develop prescription guidelines for burning these stands that utilize this information to minimize overstory mortality.
3) Describe stand structure and composition of long-unburned longleaf pine stands.
4) Survey mortality resulting from re-introduction of fire into long-unburned stands.
5) Track foliar and root dynamics and southern pine overstory mortality associated with re-introduction of fire.
6) Examine the mechanistic relationship between duff consumption and pine mortality.

METHODS

ASSESSMENT OF LITERATURE

We reviewed the literature to examine whether a pattern exists for high longleaf pine mortality in long-unburned stands following smoldering that is supported by accumulated organic material on the forest floor. These literature reviews are included in APPENDIX A (published in the journal *Restoration Ecology* 13:1-9) and B.

FOFEM MODELING

We also compared modeled fire effects to empirical results in large landscape fires and small individual tree burning in long-unburned longleaf pine forests. We predicted that current models developed for pristine ecosystems would perform poorly when compared with previously, but now more common, forests. FOFEM 5.2.1, a common tool for fire and restoration managers (e.g., Agee 2003, Reinhardt 2003), was selected for analysis using inputs from field burns in an on-going project. Specific hypotheses were: 1. mortality estimates would be poor in fire excluded stands, since second-order effects dominate these fires; 2. estimates of fuel consumption, since based on physical models, would model well in fire excluded stands; and 3. estimates of soil heating, since the product of uncharacteristic changes due to fire exclusion, would be underestimated by current model output. These results should both assist restorationists and managers in longleaf pine ecosystems and help identify patterns that may hold in other fire-excluded forests. This work is important for evaluating the utility of current predictive models and to elucidate improvements to invigorate these important decision-support tools (Appendix C).

SITE INFORMATION

We conducted experimental burns in four long-unburned (35 to 45 years since fire) longleaf pine forests at Eglin Air Force Base on the Florida Panhandle, (Okaloosa Co., FL USA; Figure 1). All stands had heavy downed woody and duff fuel loading (ranging from 14 to 34 tons ha^{-1}), remnant longleaf pine overstory (45-200 trees > 10 cm DBH ha^{-1}), and altered midstory and canopy tree species composition typical of long-unburned pine forests of the southeastern Coastal Plain (Gilliam and Platt 1999, Kush and Meldahl 2000). All sites are within the Southern Pine Hills District of the Coastal Plain Physiographic Province with deep, well-drained sandy soils (Brown et al. 1990). Soils of the study sites were all typic quartzipsamments of the Lakeland series with mean depth to water table exceeding 200 cm (Overing 1995). The climate of the area is subtropical, characterized by warm, humid summers and mild winters, with mean temperatures of 25° C and mean annual precipitation of 1580 mm, most of which falls from June to September (Overing 1995). Elevations of the study sites are 52-85 m asl and all sites have typical sandhill topography with minimal effects of slope and aspect (Myers 1990).

The individual tree experiment and one validation burn were conducted in a long-unburned (37 years since fire) longleaf pine stand at the Ordway-Swisher Memorial Preserve (Putnam Co., Florida, USA; Figure 1). This preserve is) managed cooperatively by the University of Florida and The Nature Conservancy. The stand was dominated by an overstory of longleaf pine, with a thick midstory of oaks (*Quercus laevis, Q. geminata,* and *Q. hemisphaerica*), a patchy remnant groundcover dominated by *Aristida stricta*, and a thick forest floor (depths to 15 cm) typical of long-unburned xeric southeastern pine ecosystems (Varner et al. 2005). Soils of the site are deep, extensively well-drained hyperthermic, uncoated Lamellic Quartzipsamments in the Candler series (Readle 1990). The topography is gentle, with gentle north-facing slopes < 5% and elevations averaging 16 m above msl. The climate is humid, subtropical with long, warm, and humid summers and short, mild winters with annual temperatures and precipitation averaging 20º C and 1432 mm, respectively (Readle 1990).

We also conducted validation burns in two additional long-unburned (ca. 35 to 45 years since fire) longleaf pine forests in the southeastern US to begin to validate our model for reducing duff while maintaining overstory pines. Sites were located at:

(1) Moody Forest Natural Area (Appling County, Georgia) managed by The Nature Conservancy, WET validation; and
(2) Fort Gordon Military Reservation (Richmond County, Georgia) managed by the Department of Defense, MOIST validation.

The DRY validation burn was conduced at the Ordway-Swisher Memorial Preserve described above. These sites were selected to represent a variety of management objectives (endangered species conservation, timber production, restoration of presettlement structure and composition), ownerships (State- Nature Conservancy, Department of Defense, and University-Nature Conservancy), and site conditions (mesic productive clayhills to xeric sandhills) typical of remnant fire-suppressed southern pine stands.

DATA COLLECTION

Please refer to appendices for more detail on site selection for the individual components of this study.

Weather Measures

Six weather stations were set up in 2001 for varying lengths of time to monitor conditions at the Ramer Tower site at Eglin Air Force Base. One of these stations, Eglin 1, was left in place to monitor the 2002 burns and as of August 2005 is still collecting data. Two weather stations (Eglin 12 and 13) were set up at Ranger Camp in January of 2002 and collected data until May 2003. The stations at Eglin 1, 12, and 13 provide the longest and most complete data record available.

All weather stations measured air temperature, relative humidity, wind speed, and wind direction. Additionally, stations 1, 12 and 13 measured 10 hour fuel temperature, 10 hour fuel moisture, barometric pressure, and precipitation. Sensors at all stations had a sampling interval of 10 seconds and logged data averages every 15 minutes.

Forest floor moisture was monitored at all stations using Campbell Scientific model CS-615 time-domain reflectometer (TDR) probes. These TDRs consisted of two parallel wave guides 3.2 mm in diameter, 30 cm long, and 3.2 cm apart (Appendix D).

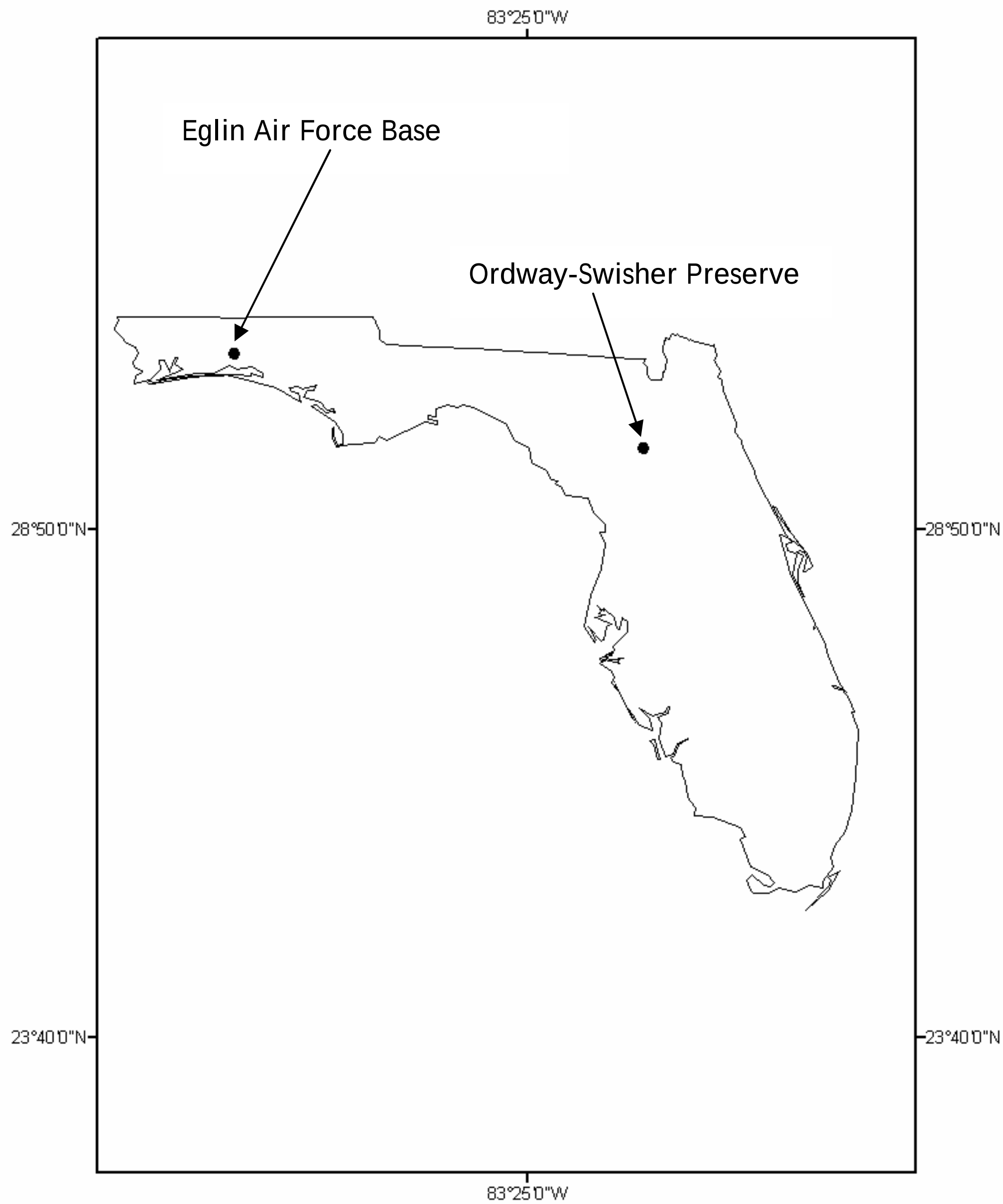


Figure 1. Location of study sites in northern Florida, USA. Both sites had undergone 37-40 y of fire exclusion prior to prescribed and simulated fires. Operational prescribed fires were conducted at Eglin Air Force Base. Small individual tree fires to evaluate mineral soil heating were conducted at the Swisher-Ordway Preserve.

Mortality Study and Prescription Validation Burns

For the mortality study four 10 ha stands at each of four sites at Eglin AFB were randomly assigned to one of four prescribed fire treatments based on day-of-burn volumetric duff moisture content (vdmc; percent of dry weight): dry (60% vdmc); moist (90% vdmc); wet (120% vdmc); and a no-burn control. For each experimental fire, we recorded fire weather, fuel moisture, and fire behavior. All prescribed burns were ignited during the late dormant season (February to April). To minimize variation in fire behavior, all fires were ignited using strip head fires or spot-grid ignition (Wade and Lunsford 1989), with ignition managed to minimize variation in flame lengths and rate of spread.

The experimental design of the validation burn sites was based on our Eglin AFB study, with 50 trees selected at random for measures of forest floor depth, moisture content, smoldering consumption, and tree mortality. Burns at all three sites were based on day-of-burn duff moisture content (dmc; percent of dry weight): dry (60% dmc); moist (90% dmc); and wet (120% dmc). For each experimental burn, we recorded fire weather, fuel moisture, and fire behavior. All prescribed burns were ignited during the late dormant season (February to late March). All fires were ignited using strip head fires or spot-grid ignition with width between strips adjusted to minimize variation in fire behavior.

Characteristics of ground fuels and vegetation were measured in each plot prior to burning. Within each replicate plot, we randomly selected 50 pines with > 20 cm dbh for fire effects sampling. We measured forest floor depth by horizon (litter [Oi horizon] and duff [Oe and Oa horizons]) at the base of each of the selected trees. In each plot we estimated total woody fuel loading using Brown's (1974) planar intercept method. Forest floor depth was measured at each tree using eight 20 cm pins buried flush with the litter surface and offset from the stem approximately 10 cm at cardinal and ordinal directions. Within 5 cm of each pin, the composition (material and depth of Oi, Oe, and Oa forest floor horizons) was described with little disturbance to the fuelbed. For all overstory pines (> 15 cm dbh; dbh =stem diameter at 1.37 m), we recorded their dbh, total height, crown height, and distance and direction to plot centers.

Initial post-burn measurements were made on all trees 3 to 4 weeks following the experimental fires. Stem char height (in cardinal directions at each tree) was measured on all trees with a height pole at four cardinal directions. Scorch height, maximum height of needle consumption, and percent of canopy volume scorched were estimated on all plot trees using a clinometer. Post-fire reductions in forest floor depth at individual trees were measured as the average difference between the pre- and post-fire exposure of duff pins. Basal damage and evidence of pathogens were noted for all plot trees. Following initial post-burn surveys, we surveyed tree mortality and any signs of decline or disease 6, 12, 18, and 24 months post-burn to capture the temporal patterns of mortality.

For all 2002 burns, rates of radial stem growth were determined for 15 trees two years following burns. From each randomly selected tree per plot, we extracted two 5 cm cores at 1 m height using an increment borer. Two cores per tree were extracted to better detect locally absent rings. All cores were dried, mounted, and sanded according to standard dendrochronological techniques prior to measurement (Stokes and Smiley 1968, Fritts 1976). Ring width was measured to the nearest 0.01 mm using a binocular microscope. Ring width was determined for the two years prior to burns (2000-2001) and the two years following burns (2002-2003). (Appendix E).

Individual Tree Studies

One meter radius plots were established surrounding 80 randomly selected mature (30 – 50 cm DBH) individual longleaf pines at the Ordway-Swisher Memorial Preserve. Four treatments (20 replicates per treatment) were installed in a completely randomized design that examined three hypothesized causes of post-fire mortality: 1) root damage (ROOT); 2) root and stem damage (ROOT+STEM); 3) stem damage (STEM); and 4) a control treatment that burned, but was extinguished prior to smoldering phase combustion (CONTROL). Root damage treatments were accomplished by allowing forest floor combustion while protecting the basal bark with fire retardant material (Cleveland Laminating Corp., Cleveland, OH, USA) sheathed over 15 cm high aluminum flashing embedded 10 cm from the basal bark (Figure 2). In the ROOT+STEM treatment, fires were allowed to heat both basal bark and duff and underlying roots. STEM treatments heated basal bark, with the adjacent forest floor protected from fire by wrapping fire retardant material around embedded 15 cm high aluminum flashing. CONTROL burns were extinguished with a flapper once flaming fire subsided.

Since mortality following basal damage is delayed in longleaf pine (Varner et al. 2005), two surrogates were used to approximate tree stress: radial growth (Busse et al. 2001) and root non-structural carbohydrates (Wargo et al. 1972, Marshall and Waring 1985, Kozlowski and Pallardy 1997). Radial stem growth (mm) of all 80 treatment trees was measured using increment cores (2 per tree, 90º apart) extracted one year post-burn (January-February 2005). Cores were air-dried, mounted, and sanded according to standard dendrochronological methodology (Stokes and Smiley 1968). All cores were measured using a binocular microscope with both earlywood and latewood measured to the nearest 0.01 mm.

Within a randomly selected subset of 8 trees in each burning treatment, we sampled total non-structural carbohydrate concentrations (starch + sugar) in roots immediately post-fire to document the carbon status of the tree within 10 days following burns and at 4 months post-burn. For each of the root carbohydrate samples, we collected 3 g of 1-2 mm diameter roots and 3 g of 2-5 mm longleaf pine roots from the surficial mineral soil horizon surrounding experimental trees. All roots were bagged and immediately stored on dry ice in the field, then transported to the laboratory within 8 hours. Immediately upon removal from chilling, the roots were rinsed and oven-dried at 100° C for 2 h, followed by drying at 70° C to a constant mass, minimizing post-harvest carbohydrate losses (Caldwell 1989). Root non-structural carbohydrate samples were analyzed using a modified phenol-sulphuric acid method (Buysee and Merckx 1993).

To understand the role of fuels on fire intensity and tree damage, we measured the basal forest floor consumption surrounding each treatment tree. Eight 20 cm tall steel pins were installed flush with the forest floor 8 cm from the stem in cardinal and ordinal directions. Following all burns, pins were measured for depth reduction [(initial depth - post-fire depth) / initial depth]. To estimate horizon moisture content, forest floor fuels were collected each burn day in by horizon from trees proximal to treatment trees. Samples were divided along horizons, with Oi removed first, then Oe material, concluding with Oa fuels. Since pine cones are likely vectors of duff ignition (Fonda and Varner 2005), six pine cones (3 recent, 3 decomposing) within the drip line of the source tree were collected and sealed in 4 mm polyethylene bags. In the laboratory, all fuels were oven-dried at 70° C to a constant weight to determine moisture content and dry biomass.

Fire temperatures were measured on a subset of all treatment trees during fires using Type J (range 0º to 1200° C) thermocouples connected to a Campbell Scientific CR10X datalogger. Temperature was measured on the bark surface at three points 120º apart at the forest floor-bark interface and at DBH (1 point). To assess root and soil heating, thermocouples were buried 120º apart in the lower duff (Oa horizon; 3 points), and directly beneath these points in the mineral soil at 5, 10, and 20 cm depths (9 points). Temperature was measured every two minutes from 15 minutes pre-ignition through the duration of the burning day (termination was required by 1700 hours on all burning days except the 4 November fire). (Appendix F).

RESULTS

Objective 1: Determine threshold moisture conditions that initiate and maintain smoldering combustion within the forest floor of longleaf pine stands and to document the consequences of this combustion for overstory tree mortality. (Appendix D).

For each prescribed fire, pre- and post-burn fuel loadings were measured at a set of 30 plots per unit set in a 1 chain (66-foot) grid. The fuel loadings in the forest floor organic layer are the only ones used in this study. By conducting prescribed burns on adjacent units under differing moisture conditions, a range in forest floor consumption was achieved. Duff consumption amount and relative TDR duff moisture level at the time of ignition were significantly correlated. Using this relationship, burn thresholds were defined at the upper and lower limits of the TDR measured moisture indexes. These thresholds correspond to the wettest (least overall consumption) and driest (most overall consumption) fires at the Ramer Tower site in 2001 and at the Ranger Camp site in 2002. These thresholds do not however represent the full range within which prescribed burning occurs. Observed data are posted to the website www.fs.fed.us/PNW/AIRFIRE/fm each day so that burn managers in the area can track the moisture index as it relates to these thresholds and anticipate whether maximum or minimum consumption may occur based upon observed moisture levels.

The approach developed in Ferguson et al. (2002) was used to fit a model relating duff layer moisture to precipitation and moisture data. 1300 LST values were used to filter out the diurnal cycle and to create a model consistent with the National Fire Danger Rating System, which uses 1300 LST observations to calculate its indexes. Many predictors, including past 24-hour average relative humidity, past 24-hour average 10 hour fuel moisture, past 24-hour precipitation duration, and past 48-hour precipitation were tested in multiple linear regressions. As in Furguson et al. (2002), the three predictors used in the litter equation yielded the highest r^2 and correlation values for a prediction of the duff layer moisture. Some predictors, such as past 24-hour precipitation duration, also fit quite well, but the correlation values were not as high as for the total past 24-hour precipitation amount. A multiple linear regression of the moisture index with the previous day's moisture index, the square root of the past 24 hour precipitation, and the square root of the precipitation from the previous 24 hour period has an r^2 value of 0.9997 and a correlation value of 0.95. The prediction works well during dry periods but has some trouble accurately capturing wetting periods. Overall, the mean absolute error for the model is 0.0080. Separating the days with rain from the days without rain gives an idea of the differing model performance for the two phases. Mean absolute error is 0.0037 for days without rain and 0.0135 for days with rain.

Visual inspection of the time series of the moisture index and precipitation indicated an inconsistent moisture index response for any given amount of rain. We hypothesize that a short intense rainfall is less effective at wetting the forest floor than a longer, less intense rain event of the same magnitude. Additionally, it appears that the forest floor organic layers are somewhat hydrophobic when the moisture index drops to very low levels. When the forest floor is very dry, it appears to require an as-of-yet unquantified volume of rain for the moisture index to noticeably respond. These differing trends in forest floor wetting are likely to be the cause of the poorer model performance on days with rain as opposed to rainless days.

To further test the application of this type of predictive model, multiple linear regressions were performed using data from weather stations Eglin 12 and Eglin 13. These regressions were based upon data from 2002 and 2003. Again predictive equations were developed that were consistent in accuracy with the Eglin 1 predictions. Some of the same patterns were also found. The same predictive variables yielded the highest correlation, and drying was better predicted then wetting.

Objective 2: Develop prescription guidelines for burning these stands that utilize this information to minimize overstory mortality.

From the curvilinear relationship between mortality and duff moisture, we have identified clear thresholds of duff moisture that correspond to high probability of consumption and thus the high risk of overstory mortality. During the Eglin AFB research effort, only 24 days over a 14 month study period produced safe duff burning conditions, and only 9 of those days were free from rain events. While the actual number of days may vary considerably from year to year depending upon cycles of drought and hurricane activity, the conditions whereby duff is saturated and desiccates are likely independent from those climatic cycles (i.e., the frequency of days where safe burning condition exist will vary from year to year, but the actual amount and duration of rain driving safe burning conditions should be consistent among years.).

Modeling efforts to date on this project suggest that four primary variables contribute to the development of safe duff burning prescriptions: evapotranspiration, previous rainfall magnitude, previous rainfall duration, and the preceding month total rainfall. Analysis of those days where safe duff burning conditions were observed suggest that 1 inch or 0.5 inches of rain combined with >12 hour duration of rainfall will be sufficient to produce safe condition during months of low ET and normal climatic rainfall. During months of high ET, results suggest that >1.5 inches or 1 inch of rain combined with >12 hours duration of rainfall will be sufficient to produce safe condition during normal climatic conditions. When conditions are dry, even extreme rain events cannot always saturate duff. During June of 2001, 4 consecutive days of rain totaling nearly 2 inches were not enough to produce safe burning conditions due to the preceding month's dryness and high ET during the month of June (Figure 2).

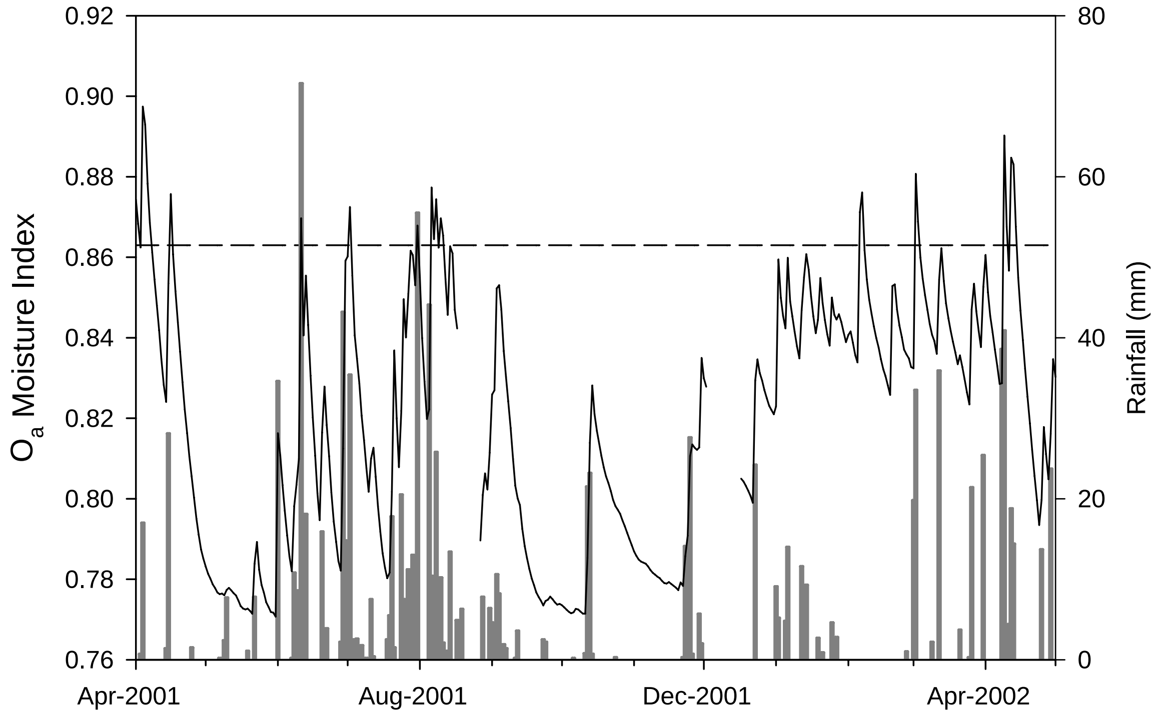


Figure 2. O_a Moisture Index (solid line) plotted against rainfall (gray bars). The horizontal dashed line represents the O_a moisture threshold. Gaps in the moisture index line indicate missing data. Rainfall data is missing for the periods 12/3/2001 to12/16/2001 and 1/31/2002 to 2/20/2002. A total of twenty-four days had an Oa moisture index above the threshold, nine days of which also had no rainfall.

In addition to these independent weather parameters, this study produced a duff moisture website and calculator at the following website for managers to use in combination with duff moisture CS-615 probes on Campbell Scientific Weathers stations: http://www.fs.fed.us/pnw/airfire/fm/. This calculator (Figure 3) allows managers at Eglin AFB and surrounding areas to quickly determine from probe values on site whether conditions are safe to burn. While this tool is somewhat limited in the geographic area that it can serve, it is a model for how managers at other large landscapes can invest in existing technology and produce a useful duff moisture calculator relevant to their fuels and site conditions.

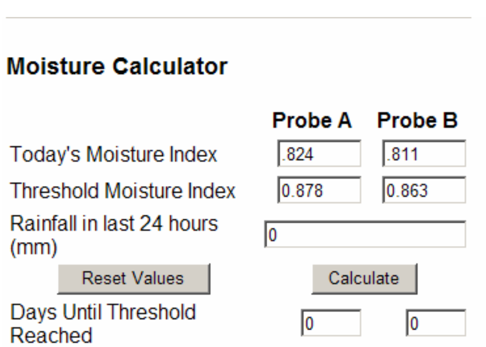


Figure 3. Duff Moisture Calculator on the Airfire web page displaying real time duff moisture values from the Eglin AFB study site.

The consumption models and forest floor loading values have been implemented into the JFSP funded national consumption software product Consume 3.0 (Ottmar 2004) which is planned for release in late summer, 2005 at www.fs.fed.us/pnw/fera. The woody fuel and duff consumption data collected from this study were used to derive coefficients for theoretical and empirical fuel consumption models for the woody fuel and forest floor fuelbed categories. Large woody fuel moisture was found to be the key variable in predicting woody fuel consumption; duff moisture content was the most important variable in calculating forest floor consumption. In addition, litter and duff bulk density samples collected during the project were used to modify forest floor loading calculations from depth measurements. Consume 3.0 will predict the overall tons per acre consumed by a fire under varying fuel moisture regimes. Such a model may be very helpful when prescription parameters and burn planning objectives are more closely tied to smoke production from smoldering fire rather than overstory mortality.

Objective 3: Describe stand structure and composition of long-unburned longleaf pine stands. (Appendices A, B)

We reviewed case studies of longleaf pine ecosystem restoration, highlighting novel fire behavior, patterns of tree mortality, and unintended outcomes resulting from reintroduction of fire. Many of these pineland restoration efforts have resulted in excessive overstory pine mortality (often > 50%) and produced substantial quantities of noxious smoke. The most compelling mechanisms of high tree mortality after reintroduction of fire are related to smoldering combustion of surface layers of organic matter (duff) around the bases of old pines. Development of effective methods to reduce fuels and competing vegetation while encouraging native vegetation is a restoration challenge common to fire-prone ecosystems worldwide that will require understanding of the responses of altered ecosystems to the resumption of historically natural disturbances.

Among the deleterious effects of fire exclusion in temperate coniferous forests is the accumulation of organic forest floor fuels. These organic forest fuels, particularly litter (Oi horizon) and duff (Oe and Oa horizons), influence fire behavior and effects. We also reviewed the literature to summarize the state of our knowledge on duff accumulation, the linkages between duff and fire effects, and primary research needs related to duff and fire-excluded temperate coniferous forests. Duff is primarily a smoldering fuel, subjecting basal vascular tissues and imbedded and underlying roots to lethal temperatures for hours to days following passage of the flaming front. Post-fire tree growth, stress, and mortality have been linked to duff smoldering throughout temperate coniferous forests. Relative to the benign emissions of flaming combustion, smoldering emissions generate noxious compounds and abundant greenhouse gases. Little is known regarding process-based duff accumulation and consumption patterns. Further work is needed on incorporating the complexity of forest floor and duff fuels into fire behavior and effects models.

Objective 4: Survey mortality resulting from re-introduction of fire into long-unburned

stands. (Appendix C, E)

Field mortality experiment (Appendix E)

Two and three years after experimental fires, overstory pines in the dry treatments (moisture content 60% of dry weight) suffered the greatest mortality (mean = 20.5%), whereas the wet (120% moisture content); and moist (90% moisture content) treatments did not differ from the unburned control treatment in pine mortality (0.5 % and 1.0 % vs. 3.0 %, respectively). Across the treatments, fire-induced reductions in duff depth were greatest in the dry treatment, averaging 3.8 cm (46.5%) consumed compared with the moist (1.4 cm, 14.5%) and wet (0.6 cm, 5%) treatments. In a logistic regression model with individual trees nested within our three burning treatments, the best predictors of individual pine mortality were duff consumption and percent of canopy scorched ($P< 0.001$; $R^2= 0.34$). In this model, canopy scorch was only significant in the dry burning treatment, while duff consumption was significant across all treatments. Duff consumption was related to pre-burn lower duff (Oa) fuel moisture content ($R^2 = 0.78$, $P <0.001$). Restoration and management of fire-excluded longleaf pine forests will require development of burn prescriptions that include both the effects of flaming combustion and residual smoldering fires, critical fire effects in these fire-excluded coniferous forests.

Validation burns

In both the wet and moist validation burns, no mortality occurred over the 18 month study period, a strong validation of our prescription. Post-burn mortality at the Ordway dry burn was 8% after the first 12 months; two additional pines died due to lightning strikes. This low mortality was within the range we observed at Eglin Air Force Base. Annual pine mortality surveys should continue five years post-treatment (until October 2008).

During experimental burning we were able to interact with regional managers about the problems associated with duff smoldering and southern pine mortality. At the Moody Forest Natural Area validation, we transferred information and study status to personnel from The Nature Conservancy, Georgia Department of Natural Resources, US Department of Defense, as well as through coverage by the state-wide media. In the validation at the Ordway DRY burn, we discussed the phenomenon with personnel from The Nature Conservancy, St. John’s River Water Management District (State of Florida), and University of Florida.

Simulation model results (Appendix C)

Simulated mortality in a modeling effort resulted in lower estimated mortality in long-unburned longleaf pine stands than found from field experiments under all burning conditions. FOFEM predicted 35 % overstory mortality across all moisture scenarios. In field burns, there was no overstory pine mortality during the first year following burns; during the second year, mortality was 0.5, 3.0, and 20.5 % in the wet, moist, and dry scenarios, respectively. In simulations of all moisture scenarios, probability of tree mortality decreased with increasing tree diameter. In observed field burns, mortality probabilities were uniform in wet burns, concentrated in smaller trees in moist burns, and concentrated in larger pines in dry burns.

Duff consumption and smoldering times were greater in field burns that in simulations. FOFEM predicted no duff consumption in the wet and moist burns, and only 8.1% in the dry scenario. Field burns resulted in duff consumption across all moisture scenarios; average duff consumption ranged from 5.0 - 46.5% in the wet to dry burns. Similarly, FOFEM predicted short smoldering times, while field observations were longer, particularly in the dry scenario. Smoke emissions for the simulated burns were predictably highest in the dry burns, with particulate matter (both PM_{10} and $PM_{2.5}$) much higher in the dry burns than either the moist or wet scenarios. No smoke emissions were measured in field burns, but since large fractions of smoke output are generated by smoldering, these values would be expected to increase substantially in field burns where smoldering times were prolonged.

Simulations did not predict any mineral soil heating above lethal temperatures (>60° C). Field burns surrounding individual pines, however, resulted in mineral soil heating across all moisture scenarios and to depths of 20-cm in mineral soil. Dry burns resulted in elevated temperatures at all depths measured.

These results indicate that model validation is necessary across the variation present in contemporary landscapes. While FOFEM did not well characterize the fires tested here, the weaknesses revealed help identify gaps in both empirical and theoretical models. Incorporation of characteristics based on fuel properties will improve these models in site-specific fires and increase our understanding of the effects of fires on increasingly different ecosystems.

Objective 5: Track foliar and root dynamics and southern pine overstory mortality associated with re-introduction of fire. (Appendix F)

While we found no tree mortality, there was significant variation in radial growth in the individual tree study one-year following burning. Radial growth did not differ among treatments (P=0.58), but growth was related to heating duration across treatments. In a step-wise regression, radial growth (% change from 2003 ring radius) was related to heating duration > 60º C within the top 5 cm of mineral soil (P = 0.08, R^2 = 0.16 5). Earlywood increment was insensitive to heating durations, but step-wise regression analysis found an inverse relationship between latewood growth and 10-cm mineral soil temperatures > 60º C (P=0.069; R^2 = 0.17).

Like radial growth, root carbohydrate levels were independent of the stem, root, root+ stem or control burning treatments. Fine (1-2 mm diameter) pine root carbohydrates were insensitive to heating durations. However, heating durations across treatments negatively influenced coarse root carbohydrate supplies. Heating > 60º C at 5 cm depth in the mineral soil caused carbohydrate drain (P<0.01), explaining 59% of the variation in post-burn changes in coarse root carbohydrates.

Among the most striking results from this experiment was the depth and duration of heating in the lower duff and mineral soil. Across all smoldering treatments, duff temperatures were elevated above ambient (23º C) temperatures. This finding is significant given that in long-unburned longleaf pine stands targeted for restoration, roughly half of all fine roots grow within basal duff (Gordon and Varner 2002) and the proximity of the underlying roots in the surface mineral soil (Heyward 1933). Mineral soil heating, the most prominent predictor of reductions in growth and stored carbohydrates, was above > 60º C in the top 5-cm in 58% of all burns (75% of treatments designed for root heating), as well as in lower depths: 42 and 25% of all burns propagated temperatures > 60 º C to depths of 10- and 20-cm below the surface, respectively. In the only overnight burn (4 November 2003; all other burns were extinguished according to prescription), temperatures in the mineral soil were maintained above lethal levels overnight, perhaps indicative of how other trees would have burned if not extinguished and how fuels smolder in actual fires.

Changes in root carbohydrates found in this study strongly support the role of mineral soil heating as the primary culprit of post-fire tree stress. Whereas stem radial growth in longleaf pine represents an aggregate of both the current and preceding year's stresses (Meldahl et al. 1999), carbohydrate supplies are metrics of current tree stress (Wargo et al. 1972, Marshall and Waring 1985, Dunn and Lorio 1992, Kozlowski and Pallardy 1997, Guo et al. 2004). Long duration lethal heating at 5 cm depths explained 59% of the variation in post-burn changes in coarse root carbohydrates, support for root heating as a cause of overstory tree stress, and potentially the widespread mortality reported following restoration fires region-wide (Varner et al. 2005).

Objective 6: Examine the mechanistic relationship between duff consumption and pine mortality. (Appendices F, G)

We burned 80 mature *Pinus palustris* in a randomized experiment testing the effects of basal burning treatments (long-duration heating to stem vascular meristems, surficial roots, combinations of the two, and a non-smoldering control) and lethal temperature durations on subsequent pine radial growth and root nonstructural carbohydrates. Duff and mineral soil temperatures in the experimental fires were consistently above lethal temperatures (> 60º C) for hours following ignition, with values above 60º C recorded to 20 cm below the mineral soil surface. Post-fire changes in radial growth were related to duration of temperatures > 60º C in the upper 5-cm of mineral soil ($P = 0.08$) and changes in latewood increment in the year following fires was related to duration of temperatures > 60º C at 10-cm depths within the mineral soil ($P = 0.05$), but neither explained much of the variability in post-fire growth ($R^2 = 0.16$ and 0.17 for radial and latewood growth, respectively). In contrast, changes 120 days following burning in nonstructural carbohydrate content in coarse roots (2-5 mm diameter) were strongly linked to 5-cm mineral soil heating duration ($P<0.01$; $R^2 = 0.59$). Results from this study implicate the role of mineral soil heating, not basal girdling, in the post-fire decline of longleaf pine.

This experiment examined burning characteristics of pine cones as a separate fuel component. Cones of fire resisters ponderosa pine, Jeffrey pine, longleaf pine, and south Florida slash pine, and cones of fire evaders Monterey pine, knobcone pine, sand pine, and pond pine were burned in a fire chamber. The experiment tested fire adaptive strategy (resisters vs. evaders), geographic region (western vs. eastern U.S.A.), and interactions between those two factors in a 2x2 factorial experiment. Jeffrey pine, longleaf pine, and south Florida slash pine supported the longest flames, smolder times, and burn times; they also lost >89% of cone mass. Monterey pine and knobcone pine sustained flames that lasted >10 min. Cones of Monterey pine, sand pine, and pond pine lost <50% cone mass. Resisters significantly exceeded evaders in all burning categories except flame time and mean rate of weight loss. Western pines significantly exceeded eastern pines in all burning categories except flame length and percent fuel combusted. Significant interactions between fire adaptive strategy and geographic region existed for all burning characteristics except mean rate of weight loss. The interaction was accounted for by cones of eastern evaders, which had the lowest mean values for most characteristics. Only recently have cones been regarded as a separate fuel component, yet they contribute more to fire regimes in their communities than previously thought. Fire models might be more accurate if they incorporate the contributions of cones to fire regimes. Furthermore, smoke emitted by smoldering cones is an important smoke management concern.

DELIVERABLES

The primary deliverable products for the project included two peer reviewed manuscripts, a website, prescription parameters for avoiding duff consumption, updates to CONSUME 3.0, and technology transfer through outreach; see Table 1 for list of deliverables.

Annual Progress Reports are in Appendix H.

PUBLICATIONS

Varner, J.M., D.R. Gordon, F.E. Putz, and J.K. Hiers. 2005. Novel fire effects in southeastern pine forests: smoldering fire and overstory pine mortality. *Restoration Ecology* 13:1-9.

Fonda, R. and J.M. Varner. 2005. Burning characteristics of cones from eight pine species. *Northwest Science* 78:322-333.

Varner, J. M. 2004. Fuels of southeastern wildlands. USDA Forest Service Encyclopedia of Southern Fire Science. http://www.forestryencyclopedia.net/Encyclopedia/Fire%20Science .

Varner, J. M. 2004. Fuel consumption. USDA Forest Service Encyclopedia of Southern Fire Science. http://www.forestryencyclopedia.net/Encyclopedia/Fire%20Science .

Table 1. Comparison of proposed and actual deliverables.

Proposed	Delivered
Study implementation documents: -Literature Review -Detailed Study Plan -2 Progress Reports -Final Report	Literature Review was published as: Varner, M.J., III, D.R. Gordon, F.E. Putz, and J. K. Hiers. 2005. Restoring fire to long-unburned *Pinus palustris* ecosystems: Novel fire effects and consequences for long-unburned ecosystems. Restoration Ecology 13: 1-9.
Datasets: -Pre- post- treatment datasets for fuels, -weather, -consumption, -mortality	All complete and published to FRAMES site with complete metadata records. http://frames.nbii.gov/portal/server.pt
-Consume 3.0	All consumption data have been included in CONSUME 3.0 released by PNW Research Station. Variability in duff consumption necessitated comparisons to western datasets for more robust predictions.
2 Manuscripts	2 manuscripts were produced for peer reviewed journals; 4 additional manuscripts in preparation; multiple additional publications (see below).
1 Website	http://www.fs.fed.us/pnw/airfire/fm/
1 Outreach newsletter	Results published in 3 newsletters Longleaf Alliance Newsletter, Society for Ecological Restoration Coastal Plain Chapter (Fall 03), and the Georgia Chapter of The Nature Conservancy annual newsletter (2003).
Field tours of study site	3 field tours of the study site with the Society for Ecological Restoration, Fire Learning Network, and Florida Division of Forestry.
Demonstration burns	Three demonstration burns were successfully conducted to test prescription parameters at Moody Natural Area (Baxley, GA), Ft. Gordon (Augusta, GA), and Ordway-Swisher Preserve (Melrose, FL).
Prescription Guidelines for safely burning duff	Results are being incorporated into third edition of Guide to Prescribed Burning in Southern Forests (Wade and Moorehead 2005 in prep). Brochure on prescriptions for fires in high duff systems developed.
Not proposed	Manuscript on duff characterization
	Manuscript on pyrogenicity of longleaf pine cones and their role as fuel vector for ground fire.
	Manuscript modeling weather conditions and duff moisture.
	Manuscript on physiological response of longleaf pines to root loss, canopy scorch, and basal scarring.
	9 poster presentations and published abstracts.
	5 presentations at conferences and seminars as individual presenters and/or panelists.

Hiers, J.K., R. D. Ottmar, J. J. O'Brien, J. M. Varner, III, F. E. Putz, D. Gordon, and S. Ferguson. 2003. Correlates of tree mortality resulting from re-introducing fire to long-unburned longleaf pine forests. Section P3.11 in 2nd International Wildland Fire Ecology and Fire Management Congress, Orlando, FL. http://ams.confex.com/ams/FIRE2003/techprogram/paper_67158.htm

Anderson, C., S. Ferguson, M. Rorig, K. Hiers, S. McKay, M. Moore, D. Olson, D. Wright, C. Wright, B. Vihnanek, and R. Ottmar. 2003. The influence of weather on combustion limits in a longleaf pine forest. Section J6E.2 in 2nd International Wildland Fire Ecology and Fire Management Congress, Orlando, FL. http://ams.confex.com/ams/pdfpapers/66489.pdf

Varner, J., Putz, F., Gordon, D., Hiers, K., Mitchell, R., Ottmar, R. 2003. Restoring fire to long-unburned old-growth southeastern pine savannas: new approaches for novel forests. Ecological Society of America Bulletin. Abstract. Savannah, GA.

Ferguson, S A., Ruthford, J. A., McKay, S. J., Wright, D., Wright, C., and Ottmar, R.. 2002. Measuring moisture dynamics to predict fire severity in longleaf pine forests. International Journal of Wildland Fire. 11:267-279. http://www.fs.fed.us/pnw/fera/publications/abstracts/IJWF_duff_moisture_abstract.pdf

Varner, J.M., D.R. Gordon, F.E. Putz. 2002. Forest floor structure and composition in long-unburned longleaf pine forests: implications for reintroduction of fire. Society for Ecological Restoration Coastal Plain Chapter Newsletter 2(1):4.

WEB PAGE

A web page including project progress, citation and ordering information was established at: http://www.fs.fed.us/pnw/airfire/fm/

Also see: Ottmar, R.D. 2004. Modification and validation of fuel consumption models. Progress report on file: http://jfsp.nifc.gov/JFSP_Project_Info.htm

LITERATURE CITED

References contained in Appendices.

APPENDIX A.

RESTORATION ECOLOGY 13: 1-9

Restoring fire to long-unburned *Pinus palustris* ecosystems: Novel fire effects and consequences for long-unburned ecosystems

J. Morgan Varner, III[1,5], Doria R. Gordon [2,3], Francis E. Putz [3], and J. Kevin Hiers [4]

[1] School of Natural Resources & Environment, University of Florida, Gainesville, FL, USA
[2] The Nature Conservancy, Gainesville, FL, USA
[3] Department of Botany, University of Florida, Gainesville, FL, USA
[4] Eglin Air Force Base, Jackson Guard, Niceville, FL, USA

[5]**Current address and Author for all correspondence**:
J. Morgan Varner, III
Department of Forestry and Watershed Management
Humboldt State University
1 Harpst Street
Arcata, CA 95521-8299
Tel. (707) 826-5622
Fax. (707) 826-5634
E-mail: jmvarner@humboldt.edu

Abstract

Biologically-rich savannas and woodlands dominated by *Pinus palustris* once dominated the southeastern USA landscape. With European settlement, fire suppression, and landscape fragmentation, this ecosystem has been reduced in area by 97%. Half of remnant forests are not burned with sufficient frequency, leading to declines in plant and animal species richness. For these fire-suppressed ecosystems, a major regional conservation goal has been ecological restoration, primarily through the reinitiation of historic fire regimes. Unfortunately, fire reintroduction in long-unburned longleaf pine stands can have novel, undesirable effects. We review case studies of longleaf pine ecosystem restoration, highlighting novel fire behavior, patterns of tree mortality, and unintended outcomes resulting from reintroduction of fire. Many of these pineland restoration efforts have resulted in excessive overstory pine mortality (often > 50%) and produced substantial quantities of noxious smoke. The most compelling mechanisms of high tree mortality after reintroduction of fire are related to smoldering combustion of surface layers of organic matter (duff) around the bases of old pines. Development of effective methods to reduce fuels and competing vegetation while encouraging native vegetation is a restoration challenge common to fire-prone ecosystems worldwide that will require understanding of the responses of altered ecosystems to the resumption of historically natural disturbances.

Key words: ecological restoration, fire suppression, longleaf pine, prescribed fire, smoldering duff combustion

Introduction

Southeastern USA pine forests and savannas dominated by *Pinus palustris* (longleaf pine) and a biologically diverse understory covered an estimated 37 million ha prior to European settlement (Frost 1993). During the past centuries, southeastern forestlands have been logged, farmed, subdivided, and planted with faster-growing southern pines (Croker 1987). Remnant areas not converted have been degraded by several decades of fire suppression (Croker 1987; Frost 1993). These landscape changes caused a 97% decline in the area of longleaf pine ecosystems, making them among the most imperiled ecosystems in the United States (Noss et al. 1995).

Of the remnant area of longleaf pine ecosystems, only about half is frequently burned (Outcalt 2000), leading to substantial alterations in ecosystem structure and composition. Presettlement fire regimes were typified by short fire-return intervals (FRI = 1-5 years), low intensity surface fires ignited by lightning and late Holocene Native Americans (Christensen 1981). Fire suppression transforms these once open savanna-woodland ecosystems into closed canopy forests, with reduced floral and faunal species richness, as well as heavy accumulations of surface fuels (Heyward 1939; Engstrom et al. 1984; Mushinsky 1985; Ware et al. 1993; Gilliam & Platt 1999; Kush & Meldahl 2000; Kush et al. 2000; Varner et al. 2000; Provencher et al. 2001b). Overstory density, species richness, and basal area increase in response to fire suppression (Ware et al. 1993; Gilliam & Platt 1999; Varner et al. 2000), while understory species richness and cover decrease (Gilliam & Platt 1999; Kush et al. 2000; Varner et al. 2000). Whereas organic matter on the forest floor was scarce in presettlement ecosystems, in the absence of frequent fires there are substantial accumulations of surficial organic horizons, particularly around the bases of large pines (Heyward & Barnette 1936; Brockway & Lewis 1997; Varner et al. 2000; Kush et al. 2004).

To reverse or reduce the further decline of southeastern longleaf pine ecosystems, many fire-excluded stands with remnant mature pine overstory have been targets for ecological restoration (Hermann 1993; Landers et al. 1995; Wade et al. 1998; Provencher et al. 2001b). In long-unburned pinelands, the objectives of restoration are typically to: 1) maintain the remnant pine overstory; 2) reduce hardwood midstory; 3) enhance or re-establish native plants and animals; 4) reduce accumulated fuels; and, 5) reduce native and non-native invasive species populations (Wade et al. 1998; Varner et al. 2000; Provencher et al. 2001b). Efforts at restoring community structure and composition have generally included the complementary actions of altering species composition by removing invasive species, reducing stand density, and reducing fuel loads. In highly altered systems, reintroduction of understory species is increasingly common (Bissett 1996; Cox et al. 2004; Jenkins et al. 2004). The most common approach to restoration of long-unburned southern pine communities has been the reinitiation of historical fire regimes with prescribed fires.

Our objectives for this review are to: 1) describe the effects of fire exclusion on southern pine ecosystems, 2) review the outcomes of fire reintroduction and restoration, 3) review the hypothesized causes of restoration fire mortality of overstory pines in both the Southeast and analogous ecosystems worldwide, and 4) present a fuels-based perspective for setting restoration priorities that minimizes catastrophic overstory mortality.

Effects of Fire Exclusion on Longleaf Pine Ecosystems

Overstory responses to fire suppression

With fire exclusion, Southeastern pinelands have experienced structural and compositional shifts from open savanna-woodlands to closed canopy forests. Frequently-burned savanna structure is typified by a spatially variable but mostly open canopy with stand densities of 130 to 250 trees/ha > 10 cm dbh, and basal areas of 12 -20 m^2/ha (Wahlenberg 1946; Platt et al. 1988; Boyer 1990; Palik & Pederson 1996; Varner et al. 2003; Fig. 1a). Throughout its range, longleaf pine is mono-dominant or occurs with scattered fire-resistant oaks (primarily *Quercus geminata, Q. incana, Q. laevis, Q. margaretta, and Q. marilandica*) and hickories (*Carya tomentosa* and *C. pallida*; Peet & Allard 1993; Varner et al. 2003b). With the cessation of fire-induced mortality, the cover and density of shrubs and trees increase in the midstory and canopy (Gilliam et al. 1993; Brockway & Lewis 1997; Gilliam & Platt 1999; Kush et al. 2000; Varner et al. 2000; Provencher et al. 2001a; 2001b; Fig. 1b). The species that benefit from fire suppression include many fire-susceptible species (e.g., *Q. hemisphaerica, Q. nigra, Acer rubrum, Liquidambar styraciflua*, *Magnolia grandiflora*, and *Nyssa sylvatica*) that alter stand structure by increasing tree densities, leaf areas, and basal area. Stand composition is degraded as canopy species richness increases.

Understory responses to fire suppression

Without fire in longleaf pine ecosystems, understory communities undergo radical shifts in cover and richness. Frequently-burned pineland understory communities are among the most species-rich outside of the tropics (Peet & Allard 1993; Kirkman et al. 2001; Provencher et al. 2003). Typical burned understories contain 20 to 30 species/m^2, with dominance by bunch grasses (*Aristida stricta, Schizachyrium scoparium*, and *Andropogon* spp.), asters, legumes, and other forbs including several rare and endemic plant species (Hardin & White 1989; Peet & Allard 1993). Without fire, increased overstory and midstory canopy cover, as well as leaf litter deposition, reduce sunlight reaching the forest floor, leading to the loss of light-demanding understory grasses, forbs, and pine seedlings (Provencher et al. 2001a; 2001b; Waters et al. 2004). After several decades of fire suppression, herbaceous species richness is often <2 species/m^2, pine seedlings are lacking, and the understory becomes dominated by woody species (Varner et al. 2000; Kush et al. 2004).

Midstory responses to fire suppression

A marked change in fire-excluded pinelands is the advent of a woody midstory. Most frequently-burned pinelands, particularly on sites with high net primary productivity lack a well-developed midstory stratum (Peet & Allard 1993; Landers et al. 1995). The few native shrub and tree species present in frequently-burned pinelands include oak and hickory sprouts, *Ilex glabra* (gallberry), *Vaccinium* spp., *Serenoa repens* (saw palmetto), and isolated patches or "domes" of *Quercus geminata* (Guerin 1988; Peet & Allard 1993). Without fire, hardwoods and shrubs ascend into the midstory where they increase cover and stem density dramatically (Provencher et al. 2001b).

Forest floor characteristics after fire suppression

Frequently-burned pinelands have very little organic matter on the forest floor, except some litter (Oi horizon), but this condition is altered radically by fire exclusion. Without frequent surface fires, leaf litter, sloughed bark, fallen branches and other organic necromass accumulate and decompose into fermentation (Oe) and humus (Oa) horizons absent in frequently-burned communities (Fig. 2; Heyward 1939; Switzer et al. 1979). Roots and mycorrhizal hyphae exploit these "duff" horizons, especially near the bases of large pines where duff can accumulate to depths of 25 cm or more (Varner et al. 2000; Gordon & Varner 2002; Kush et al. 2004). Litter accumulation and duff formation further block light from reaching the forest floor (Waters et al. 2004) and may play a significant role in driving changes in nutrient cycling (Wilson et al. 2002).

Responses to Fire Reintroduction: Restoration Case Studies

Flomaton Natural Area

The Flomaton Natural Area is a 27 ha remnant old-growth longleaf pine stand in Escambia County, Alabama (31°01' N, 87°15' W). Fire had been suppressed in the stand for 45 years until 1993, when a small trash fire ignited a 3 ha stand isolated by a dirt road. The wildfire was allowed to burn out on its own with no observed canopy scorch and limited stem char (all trees < 1 m char height). For several days following the fire, smoldering continued in the deep duff that had accumulated around the large remnant pines. Smoke from these fires was problematic for local residents particularly because emissions from smoldering fires are much more hazardous to human health than relatively benign flaming-phase fire emissions (McMahon et al. 1980; McMahon 1983). Additionally, the danger of re-ignition remained high as long as smoldering continued. During the first two years after the fire, heavy mortality was observed in the overstory longleaf pines (Kush et al. 2004). Mortality was highest among large pines; 91% of the trees >35 cm dbh died. Survival was higher among small (10 - 20 cm dbh), longleaf, slash (*P. elliottii* var. *elliottii*), and loblolly pines (*P. taeda*). Most of the small trees of fire-susceptible hardwood species (primarily *Liquidambar styraciflua*, *Prunus serotina*, and *Acer rubrum*) that invaded during the fire-free period also survived the fire (Kush et al. 2004).

In response to the loss of a high proportion of the old growth pines during the 1993 fire, an aggressive ecological restoration program was initiated on the adjacent 24 ha unburned site. The restoration process began with the mechanized harvesting of all hardwood stems (primarily *Quercus* spp.) > 10 cm dbh with a Morbark three-wheeled feller-buncher (Morbark Inc., Winn, Michigan). Beginning in 1994, prescribed fires were re-introduced at a FRI of 1-3 years (Varner et al. 2000; Kush et al. 2004). All fires were ignited when duff moisture content was high (typically within 2-4 days following large rain events) and were lit to minimize fire residence time and fireline intensity. Canopy scorch was low (<20% of trees) in all fires. Even though the Oe and Oa horizons in the duff were moist when the fires were ignited, smoldering was initiated in deep duff accumulations near tree stems. Occurrences of smoldering continued to be detected for several days post-ignition, requiring repeated extinguishing with backpack, ATV, and tractor-mounted water sprayers. As a result of these efforts to control fire intensity and to extinguish duff smoldering when detected, mortality of pines in the 4 years following the fire was reduced to an annual average of 4.2% (Varner et al. 2000), still much higher than typical longleaf pine mortality (Boyer 1979; Palik & Pederson 1996), but the majority of death occurred in trees < 20 cm dbh. The fires killed several pines 50-80 cm dbh, but losses of these old pines did not exceed 2 trees ha^{-1} $year^{-1}$ (Varner et al. 2000; J.S. Kush, Auburn University, unpublished data).

Eglin Air Force Base

Eglin Air Force Base is a 188,000 ha military reservation in Okaloosa, Walton, and Santa Rosa Counties in the Panhandle of Florida (30°38' N, 86°24' W). Among the many natural plant communities at Eglin, longleaf pine communities cover approximately 130,000 ha. Many of Eglin's pinelands have experienced prolonged fire-free periods (McWhite et al. 1999; Hiers et al. 2003), leading to ecosystem conditions similar to those observed at Flomaton.

Reintroduction of fire has been the major method for restoration of longleaf pine ecosystems in Eglin (McWhite et al. 1999), but the results have been mixed. As a result of fire re-introduction at Eglin, some stands suffered 75-100 % overstory pine mortality whereas in others, pine mortality was 10% or less (McWhite et al. 1999; Gordon & Varner 2002). Aside from the need to understand the mechanisms of variation in this phenomenon, these novel fire effects in such fire dependent forests are alarming. The huge scales of the restoration efforts at Eglin preclude the individual tree treatments used at Flomaton (Hiers et al. 2004). This situation is relevant to many fire-excluded areas in the Southeast, as natural resource managers must operationally manage landscapes, rather than individual trees.

Other examples

Throughout the pinelands of the Southeast, managers have experienced problems with excessive tree mortality resulting from reintroduction of fire (Table 1; Gordon & Varner 2002). As observed at Flomaton and Eglin, pine mortality following the reintroduction of fire is usually concentrated in the largest diameter classes with greatest pre-fire duff accumulations (Varner et al. 2000). Resulting pine mortality, in combination with vigorous resprouting of competing hardwoods, prolonged fire dangers, and smoke emissions plague restoration of stands throughout the southeastern US. These unintended outcomes are major deterrents to additional restoration burning region-wide.

Cause of Pine Mortality after Fire Re-Introduction

Hypothesized mechanisms for mortality of large trees after the reintroduction of fire involve the direct effects of fire, such as root damage (Ryan & Frandsen 1991; Swezy & Agee 1991), vascular tissue damage (Martin 1963; Ryan 2000), leaf scorch (Ryan 2000; Menges & Deyrup 2001), or canopy damage (Menges & Deyrup 2001; Fig. 3). Increased insect and pathogen attack of fire-stressed trees has also been suggested as an indirect cause of post-fire mortality in these communities (Ostrosina et al. 1997; Ostrosina et al. 1999; Menges & Deyrup 2001).

Where fires have been reintroduced, tree death is reportedly correlated with damage to canopy foliage and branch meristems (Herman 1954; van Wagner 1973; Wade & Johansen 1986; Menges & Deyrup 2001; McHugh et al. 2003). Foliage scorch is considered less stressful than foliage consumption, which is generally associated with damaged branch cambia (Wade & Johansen 1986). Foliage consumption has been correlated with fire-caused mortality of slash pine in the Southeast (Johansen & Wade 1987; Menges & Deyrup 2001). Nevertheless, pine mortality following reintroduction of fire has been observed without canopy damage following restoration fires (Varner et al. 2000; Kush et al. 2004). Regardless, canopy damage may represent one of many stressors to a tree, exacerbating stem or root damage, and ultimately contributing to excessive pine mortality rates following reintroduction fires.

Post-fire tree decline and mortality can also result from fire-caused root damage (Wade & Johansen 1986; Swezy & Agee 1991; Busse et al. 2000). Lateral roots of longleaf pines are concentrated within the top 30 cm of mineral soil (Heyward 1933; Wahlenberg 1946) and in long-unburned longleaf pine forests, numerous branch roots grow up into duff horizons (Gordon & Varner 2002). In frequently-burned pinelands, soil heating and resulting root mortality are negligible (e.g., Heyward 1938). With fire suppression and duff accumulation, in contrast, pine roots in duff and in the surface mineral soil can be heated, damaged, or consumed in long-duration smoldering fires where temperatures can exceed lethal values for hours (Flinn & Wein 1977; Wade & Johansen 1986). Smoldering fires spread three orders of magnitude slower than surface fires and are typically concentrated in the lower duff (Oa horizon) beneath a thermal blanket of overlying Oe material (Hungerford et al. 1995). Although localized and small, the smoldering front transmits lethal heat loads (hours > 60° C) to 10-20 cm deep in the mineral soil (J.M. Varner, unpublished data). A similar mechanism of duff root heating has been proposed as a cause of tree death and decline in ponderosa pine stands (*P. ponderosa*; e.g., Swezy & Agee 1991; Busse et al. 2000). Given the potential physiological impairment posed by large-scale root heating and consumption, mechanisms involving root damage deserve further study.

Basal cambial damage is another proposed mechanism of tree mortality following fire reintroduction. Basal damage in tree stems can occur during surface fires and during residual smoldering of duff. During surface fires, combustion of litter causes large amounts of heat to be released close to tree stems, leading to stem char (Wade & Johansen 1986; Dickinson & Johnson 2001). Bark, especially the thick accumulations on long-unburned trees, usually insulates the cambium sufficiently against heat damage (Spalt & Reifsnyder 1962; Fahnestock & Hare 1964; Hare 1965; Reifsnyder et al. 1967; Vines 1968; Dickinson & Johnson 2001). In contrast, long-duration heating during smoldering of duff around tree bases can raise temperatures to lethal levels and cause cambial death and tree mortality (Dixon et al. 1984; Ryan et al. 1988; Ryan & Rheinhardt 1988; Dunn & Lorio 1992; Ryan 2000; Dickinson & Johnson 2001). Duff smoldering often continues for hours or days following ignition (Covington & Sackett 1984; Hungerford et al. 1995), long enough to kill the cambium under even thick layers of bark. Cambial damage, even when it does not entirely encircle the stem, is correlated with fire-caused tree mortality in other conifers (e.g., Ryan et al. 1988; Ryan & Rheinhardt 1988; Ryan 2000). Given the long-duration heating observed in reintroduction fires and the potential damage to whole-tree physiology, basal cambial damage appears to be an important mechanism of overstory pine mortality when fires are reintroduced.

Indirect effects of fire re-introduction are reflected in tree physiological stress that, in turn, renders pines susceptible to pests or pathogens. Overall tree stress may be indicated by changes in carbon balance, as indicated by stem or root tissue carbohydrate levels, by reduced resin exudation pressure, or by reduced radial growth (Kozlowski et al. 1991). Past work on southeastern (Davidson & Hayes 1999) and western USA conifers (Covington et al. 1997; Ryan 2000; McHugh et al. 2003; Wallin et al. 2003; Wallin et al. 2004) has demonstrated that increased physiological stress renders trees more susceptible to pest and pathogen attack. Re-introducing fire to long-unburned slash pine stands in south Florida led to sharp increases in both *Ips* and *Platypus* spp. beetles and subsequent overstory mortality (Menges & Deyrup 2001). It follows that if restoration burning in longleaf pinelands increases tree stress then growth and defenses would decline and pest and pathogen attacks would increase. However, in many restoration treatments (burning and thinning, thinning alone, and burning alone), resulting physiological condition varies, as does the subsequent susceptibility to decline and disease. Resin exudation pressure, a correlate of a tree's ability to defend itself from bark beetle attack (Raffa & Berryman 1983; Dunn & Lorio 1992), increases following fire re-introduction in ponderosa pine ecosystems. Tree physiological condition and growth also increase following thinning, raking, and burning in long-unburned ponderosa pine forests (Feeney et al. 1998; Stone et al. 1999; Wallin et al. 2004). However, reduced radial growth has been correlated with restoration burning in other ponderosa pine forests (Busse et al. 2000). To what degree restoration treatments in southern pine stands are effective in maintaining, improving, or reducing tree physiological conditions deserves further study, but arguably only within a mechanistic framework that links physiological response to specific tree damages and characteristics of the fuels and fire that caused the damage (i.e., heat damage from smoldering duff fire to stem vascular tissues that causes physiological impairment and reduced defense capability).

Given that evidence supports a mechanistic link between stem and / or root damage as the cause of mortality following fire reintroductions, understanding smoldering combustion appears requisite for understanding the mechanism behind tree mortality in long-unburned southern pine forests. Smoldering differs from flaming combustion by being controlled mostly by oxygen availability (as opposed to fuel availability), by lower temperatures (< 500^{o} C versus higher temperatures in flaming combustion), and by longer residence times (Hungerford et al. 1995; Miyanishi 2001). Smoldering elevates temperatures in duff, in the underlying mineral soil horizons, in roots located within these horizons, and in nearby tree stems (Wade & Johansen 1986; Ryan & Frandsen 1991; Swezy & Agee 1991; Hungerford et al. 1995; Schimmel & Granstrom 1996; Haase & Sackett 1998; Dickinson & Johnson 2001, Miyanishi 2001).

Smoldering Duff Fires and Southeastern USA Restoration

Determining the correlates and mechanisms of tree mortality following fire reintroduction should be a high priority for southeastern restoration efforts. Given that 50% of all remnant longleaf pinelands are unburned (Outcalt 2000), successful restoration burning could double the area of functioning longleaf pinelands. Landscape scale fire suppression has similarly affected other southern pinelands (dominated by *P. taeda*, *P. elliottii* var. *elliottii*, *P. elliottii* var. *densa*, and *P. echinata*; Noss et al. 1995). A better understanding of restoration burning has the potential to restore the ecological integrity of these important communities. Without a more rigorous understanding of the effects of restoration, continued reintroduction of fire will inevitably lead to more catastrophic overstory mortality and hasten the decline in southeastern pine-dominated ecosystems (Landers et al. 1995; South & Buckner 2003).

Smoldering duff and tree decline and mortality is a familiar phenomenon in ecosystems maintained by frequent fires outside of the southeastern US where, in response to fire suppression, deep organic horizons accumulate around large conifers, creating a potential for mortality when fire is re-introduced (Ryan & Frandsen 1991; Swezy & Agee 1991; Haase & Sackett 1998; Stephens & Finney 2002; McHugh & Kolb 2003). It is likely that as native ecosystems continue to be degraded by fire suppression and restoration efforts ensue, we will experience other novel disturbances that will challenge future conservation and restoration.

It is ironic that southeastern USA pinelands are imperiled by fire suppression but the reintroduction of fire often results in the death of a large portion of the residual pines. Clearly, if fire is to be a useful tool for restoring the remnant stands from which it has been excluded for decades, the fire-induced mortality problem needs to be solved. As described, consumption of novel fuels in fire excluded stands play a major role in contributing to fire-induced pine mortality. Reducing these novel fuelbeds, characterized by well-developed forest floor horizons, should be a primary restoration objective for managers attempting to reintroduce fire into excluded stands. Multiple fires over many years may be necessary for the gradual elimination of these novel fuels prior to meeting ancillary restoration objectives such as midstory reduction or understory restoration. At small scales, extinguishing duff fires can save many of the large old trees for which these ecosystems are valued, but such efforts are expensive and thus unlikely to be viable over large areas. Nevertheless, understanding the patterns and processes of duff fire-induced mortality represents an important step towards restoring and maintaining southeastern pine ecosystems as viable components in our conservation landscape.

Acknowledgments

This review was supported by funding from the Joint Fire Sciences Program through the USDA Forest Service Southern Research Station (02-1A-11330136-030). We appreciate the support of Eglin Air Force Base Jackson Guard and the School of Natural Resources and the Environment at the University of Florida. James Furman, John Kush, Alan Long, Tim Martin, Bob Mitchell, Adam Watts, and two anonymous reviewers provided valuable comments and suggestions on this manuscript.

References

Bissett, N. J. 1996. Upland restoration challenge: direct seeding of wiregrass and associated species. The Palmetto Sum:8-11.

Boyer, W. D. 1979. Mortality among seed trees in longleaf pine shelterwood stands. Southern Journal of Applied Forestry **3:**165-167.

Boyer, W. D. 1990. *Pinus palustris* Mill. (Longleaf pine). Pages 405-412 in Silvics of North America Vol. 1. Conifers. USDA Forest Service Agriculture Handbook 654, Washington, D.C.

Brockway, D. G., and C. E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. Forest Ecology and Management **96:**167-183.

Busse, M. D., S. A. Simon, and G. M. Riegel. 2000. Tree-growth and understory responses to low-severity prescribed burning in thinned *Pinus ponderosa* forests of central Oregon. Forest Science **46:**258-268.

Christensen, N. L. 1981. Fire regimes in southeastern ecosystems. Pages 112-136 in H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners, editors. Fire regimes and ecosystem properties. USDA Forest Service General Technical Report WO-26. Forest Service, Washington, D. C.

Covington, W. W., and S. S. Sackett. 1984. The effect of a prescribed burn southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. Forest Science **30:**183-192.

Covington, W. W., P. Z. Fulé, M. M. Moore, S. C. Hart, T. E. Kolb, J. N. Mast, S. S. Sackett, and M. R. Wagner. 1997. Restoration of ecosystem health in southwestern ponderosa pine forests. Journal of Forestry **95:**23-29.

Cox, A. C., D. R. Gordon, J. L. Slapcinsky, and G. S. Seamon. 2004. Understory restoration in longleaf pine sandhills. Natural Areas Journal **24:**4-14.

Croker, T.C. 1987. Longleaf pine: a history of man and a forest. USDA Forest Service Forestry Report R8– FR7. U.S. Forest Service, Atlanta, Georgia.

Davidson, J., and J. L. Hayes. 1999. Effects of thinning on development of SPB infestations in old growth stands. Southern Journal of Applied Forestry **23:**193-196.

Dickinson, M. B., and E. A. Johnson. 2001. Fire effects on trees. Pages 477-525 in E.A. Johnson and K. Miyanishi, editors. Forest fires: behavior and ecological effects. Academic Press, New York.

Dixon, W. N., J. A. Corneil, R. C. Wilkinson, and J. L. Foltz. 1984. Using stem char to predict mortality and insect

infestation of fire-damaged slash pines. Southern Journal of Applied Forestry **8:**85-88.
Dunn, J. P., and P. L. Lorio. 1992. Effects of bark girdling on carbohydrate supply and resistance of loblolly pine to southern pine beetle (*Dendroctonus frontalis* Zimm.) attack. Forest Ecology and Management **50:**317-330.
Engstrom, R. T., R. L. Crawford, and W. W. Baker. 1984. Breeding bird populations in relation to changing forest structure following fire exclusion: a 15-year study. The Wilson Bulletin **96:**437-50.
Fahnestock, G. R., and R. C. Hare. 1964. Heating of tree trunks in surface fires. Journal of Forestry **62:**799-805.
Feeney, S. R., T. E. Kolb, W. W. Covington, and M.R. Wagner. 1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson Natural Area. Canadian Journal of Forest Research **28:**1295-1306.
Flinn, M. A., and R. W. Wein. 1977. Depth of underground plant organs and theoretical survival during fire. Canadian Journal of Botany **55:**2550-2554.
Frost, C.C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Tall Timbers Fire Ecology Conference **18**:17-43.
Gilliam, F. S., B. M. Yurish, and L. M. Goodwin. 1993. Community composition of an old-growth longleaf pine forest: relationship to soil texture. Bulletin of the Torrey Botanical Club **120:**287-294.
Gilliam, F. S., and W. J. Platt. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. Plant Ecology **140:**15-26.
Gordon, D. R., and J. M. Varner. 2002. Old growth longleaf pine restoration and management. Final Report to Eglin Air Force Base Jackson Guard, Niceville, Florida. 33 p. The Nature Conservancy, Altamonte Springs, Florida.
Guerin, D. N. 1988. Oak dome establishment and maintenance in a longleaf pine community in Ocala National Forest, Florida. M. S. thesis. University of Florida, Gainesville.
Haase, S. M., and S. S. Sackett. 1998. Effects of prescribed fire in giant sequoia-mixed conifer stands in Sequoia and Kings Canyon National Parks. Tall Timbers Fire Ecology Conference **20:**236-243.
Hardin, E.D., and D.L. White. 1989. Rare vascular plant taxa associated with wiregrass (*Aristida stricta*) in the southeastern United States. Natural Areas Journal **9**:234-245.
Hare, R. C. 1965. The contribution of bark to fire resistance of southern trees. Journal of Forestry **63:**248-251.
Herman, F. R. 1954. A guide for marking fire-damaged ponderosa pine in the southwest. USDA Forest Service Research Note RM-13. U. S. Forest Service Rocky Mountain Research Station, Fort Collins, Colorado.
Hermann, S. H. 1993. The longleaf pine ecosystem: ecology, restoration and management. Proceedings of the 18th Tall Timbers Fire Ecology Conference: 30 May-2 June 1991, Tallahassee. Tall Timbers Research Station, Tallahassee, Florida.
Heyward, F. 1933. The root system of longleaf pine on the deep sands of western Florida. Ecology **14:**136-148.
Heyward, F. 1938. Soil temperatures during forest fires in the longleaf pine region. Journal of Forestry **36:**478-491.
Heyward, F. 1939. The relation of fire to stand composition of longleaf pine forests. Ecology **20:**287-304.
Heyward, F., and R.M. Barnette. 1936. Field characteristics and partial chemical analyses of the humus layer of longleaf pine forest soils. Florida Agricultural Experiment Station Bulletin 302. University of Florida, Gainesville, Florida
Hiers, J. K., S. C. Laine, J. J. Bachant, J. H. Furman, W. W. Greene, and V. Compton 2003. Simple spatial modeling tool for prioritizing prescribed burning activities at the landscape scale. Conservation Biology **17**:1571-1578.
Hungerford, R. D., W. H. Frandsen, and K. C. Ryan. 1995. Ignition and burning characteristics of organic soils. Tall Timbers Fire Ecology Conference **19:**78-91.
Jenkins, A. M., D. R. Gordon, and M. T. Renda. 2004. Native alternatives for non-native turfgrasses in central Florida: germination and responses to cultural treatments. Restoration Ecology **12**:190-199.
Johansen, R. W., and D. D. Wade. 1987. Effects of crown scorch on survival and diameter growth of slash pines. Southern Journal of Applied Forestry **11:**180-184.
Kirkman, L. K., K. L. Coffey, R. J. Mitchell, and E. B. Moser. 2004. Ground cover recovery patterns and life history traits: implications for restoration obstacles and opportunities in a species-rich savanna. Journal of Ecology **92**:409-421.
Kozlowski, T. T., P. J. Kramer, and S. G. Pallardy. 1991. The physiological ecology of woody plants. Academic Press, San Diego.
Kush, J. S., and R. S. Meldahl. 2000. Composition of a virgin longleaf pine stand in south Alabama. Castanea **65:**56-63.
Kush, J. S., R. S. Meldahl, and W. D. Boyer. 2000. Understory plant community response to season of burn in natural longleaf pine forests. Tall Timbers Fire Ecology Conference **21:**33-39.
Kush, J. S., R. S. Meldahl, and C. Avery. 2004. A restoration success: longleaf pine seedlings established in a fire-

suppressed, old-growth stand. Ecological Restoration **22:**6-10.
Landers, J. L., D. H. Van Lear, and W. D. Boyer. 1995. The longleaf pine forests of the southeast: requiem or renaissance? Journal of Forestry **93**:39-44.
Martin, R. E. 1963. A basic approach to fire injury of tree stems. Tall Timbers Fire Ecology Conference **2:**151-162.
McHugh, C. W., and T. E. Kolb. 2003. Ponderosa pine mortality following fire in northern Arizona. International Journal of Wildland Fire **12:**1-16.
McHugh, C. W., T. E. Kolb, and J. L. Wilson. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. Environmental Entomology 32: 510-522.
McMahon, C. K. 1983. Characteristics of forest fuels, fire and emissions. Paper No. 45.1 in: Proceedings of the 76th Annual Meeting of the Air Pollution Control Association, 19-24 June 1983, Atlanta, Georgia. Air Pollution Control Association, Pittsburgh, Pennsylvania.
McMahon, C. K., D. D. Wade, and S. N. Tsouklas. 1980. Combustion characteristics and emissions from burning organic soils. Paper No. 15.5 in: Proceedings of the 73th Annual Meeting of the Air Pollution Control Association, 22 -27 June 1980, Montreal, Quebec. Air Pollution Control Association, Pittsburgh, Pennsylvania.
McWhite, R. W., J. Furman, C. J. Petrick, and S. M. Seiber. 1999. Integrated natural resources transitional plan, Eglin Air Force Base, 1998 – 2001. Eglin Air Force Base, Jackson Guard, Niceville, Florida.
Menges, E. S., and M. A. Deyrup. 2001. Postfire survival in south Florida slash pine: interacting effects of fire intensity, fire season, vegetation, burn size, and bark beetles. International Journal of Wildland Fire **10:**53-63.
Miyanishi, K. 2001. Duff consumption. Pages 437-475 in E.A. Johnson and K. Miyanishi, editors. Forest fires: behavior and ecological effects. Academic Press, New York.
Mushinsky, H. R.1985. Fire and the Florida sandhill herpetofaunal community: with special attention to the responses of *Cnemidophorus sexlineatus*. Herpetologica **4:**333-342.
Noss, R. F., E. T. LaRoe, and J. M. Scott. 1995. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. U. S. Department of Interior National Biological Service, Biological Report 28. Washington, D.C.
Outcalt, K.W. 2000. Occurrence of fire in longleaf pine stands in the southeast United States. Tall Timbers Fire Ecology Conference **21:**178-182.
Ostrosina, W. J., N. J. Hess, S. J. Zarnoch, T. J. Perry, and J. P. Jones. 1997. Blue-stain fungi associated with roots of southern pine trees attacked by the southern pine beetle, *Dendroctonus frontalis*. Plant Disease **81:**942-945.
Ostrosina, W. J., D. Bannwart, and R. W. Roncadori. 1999. Root-infecting fungi associated with a decline of longleaf pine in the southeastern United States. Plant and Soil **27:**145-150.
Palik, B. J., and N. Pederson. 1996. Overstory mortality and canopy disturbances in longleaf pine ecosystems. Canadian Journal of Forest Research **26:**2035-2047.
Peet, R. K., and D. J. Allard. 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf Coast regions: a preliminary classification. Tall Timbers Fire Ecology Conference **18:**45-82.
Platt, W. J., G. W. Evans, and S. L. Rathbun. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). American Naturalist **131**:491-525.
Provencher, L., B. Herring, D. R. Gordon, H. L. Rodgers, K. E. M. Galley, G. W. Tanner, J. L. Hardesty, and L. A. Brennan. 2001a. Effects of hardwood reduction techniques on longleaf pine sandhill vegetation in northwest Florida. Restoration Ecology **9:**13-27.
Provencher, L., B. J. Herring, D. R. Gordon, H. L. Rodgers, G. W. Tanner, J. L. Hardesty, L. A. Brennan, and A. R. Litt. 2001b. Longleaf pine and oak responses to hardwood reduction techniques in fire-suppressed sandhills in northwest Florida. Forest Ecology and Management **148:**1-15.
Provencher, L., A. R. Litt, and D. R. Gordon. 2003. Predictors of species richness in northwest Florida longleaf pine sandhills. Conservation Biology **17**: 1660-1671.
Raffa, K. F., and A. A. Berryman. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). Ecological Monographs **53:**27-49.
Reifsnyder, W. E., L. P. Harrington, and K. W. Spalt. 1967. Thermophysical properties of bark of shortleaf, longleaf, and red pine. Yale University Forestry Bulletin Number 70. Yale University School of Forestry, New Haven, Connecticutt.
Ryan, K.C. 2000. Effects of fire injury on water relations of ponderosa pine. Tall Timbers Fire Ecology Conference **21:**58-66.
Ryan, K. C., and W. H. Frandsen. 1991. Basal injury from smoldering fires in mature *Pinus ponderosa* Laws. International Journal of Wildland Fire **1:**107-118.

Ryan, K. C., D. L. Peterson, and E. D. Rheinhardt. 1988. Modeling long-term fire-caused mortality of Douglas-fir. Forest Science **34:**190-199.

Ryan, K. C., and E. D. Rheinhardt. 1988. Predicting postfire mortality of seven western conifers. Canadian Journal of Forest Research **18:**1291-1297.

Schimmel, J., and A. Granstrom. 1996. Fire severity and vegetation response in the boreal Swedish forest. Ecology **77:**1436-1450.

South, D. B., and E.R. Buckner. 2003. The decline of southern yellow pine timberland. Journal of Forestry **101**:30-35.

Spalt, K. W., and W. E. Reifsnyder. 1962. Bark characteristics and fire resistance: A literature survey. USDA Forest Service Occasional Paper 193 and Yale School of Forestry. U.S. Forest Service Southern Forest Experiment Station, Asheville, North Carolina.

Stephens, S. L., and M. A. Finney. 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. Forest Ecology and Management **162:**261-271.

Stone, J. E., T. E. Kolb, and W. W. Covington. 1999. Effects of thinning on presettlement *Pinus ponderosa* in northern Arizona. Restoration Ecology **7:**172-182.

Swezy, D. M., and J. K. Agee. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Canadian Journal of Forest Research **21:**626-634.

Switzer, G. L., M. G. Shelton, and L. E. Nelson. 1979. Successional development of the forest floor and soil surface on upland sites of the east Gulf Coastal Plain. Ecology **60:**1162-1171.

van Wagner, C. E. 1973. Height of crown scorch in forest fires. Canadian Journal of Forest Research **3:**373-378.

Varner, J. M., J. S. Kush, and R. S. Meldahl. 2000. Ecological restoration of an old-growth longleaf pine stand utilizing prescribed fire. Tall Timbers Fire Ecology Conference **21:**216-219.

Varner, J. M., J. S. Kush, and R. S. Meldahl. 2003. Structure of old-growth longleaf pine (*Pinus palustris* Mill.) forests in the mountains of Alabama. Castanea **68**: 211-221.

Varner, J. M., and J. S. Kush. 2004. Remnant old-growth longleaf pine (*Pinus palustris* Mill.) savannas and forests of the southeastern USA: status and threats. Natural Areas Journal **24:**141-149.

Vines, R. G. 1968. Heat transfer through bark, and the resistance of trees to fire. Australian Journal of Botany **16:**499-514.

Wade, D. D., and R. W. Johansen. 1986. Effects of fire on southern pine: observations and recommendations. USDA Forest Service General Technical Report SE-41. U.S Forest Service Southeastern Experiment Station, New Orleans, Louisiana.

Wade, D. D., G. Custer, J. Thorsen, P. Kaskey, J. Kush, B. Twomey, and D. Voltolina. 1998. Reintroduction of fire into fire-dependent ecosystems: some southern examples. Tall Timbers Fire Ecology Conference **20:**94-98.

Wahlenberg, W. G. 1946. Longleaf pine: its use, ecology, regeneration, protection, and management. USDA Forest Service and Charles Lathrop Pack Forestry Foundation, Washington, D.C.

Wallin, K.F., T. E. Kolb, K. R. Skov, and M. R. Wagner. 2003. Effects of crown scorch on ponderosa pine resistance to bark beetles in northern Arizona. Environmental Entomology **32**:652-661.

Wallin, K. F., T. E. Kolb, K. R. Skov, and M. R. Wagner. 2004. Seven-year results of thinning and burning restoration treatments on old ponderosa pines at the Gus Pearson Natural Area. Restoration Ecology **12:**239-247.

Ware, S., C. C. Frost, and P. D. Doerr. 1993. Southern mixed hardwood forest: the former longleaf pine forest. Pages 447-493 in W.H. Martin, S.G. Boyce, and A.C. Echternacht, editors. Biodiversity of the southeastern United States: lowland terrestrial communities. Wiley, New York.

Waters, M., R. E. Will, R. J. Mitchell, and J. K. Hiers. 2004. Effects of light and litter accumulation on understory development in longleaf pine sandhill ecosystems. 89th Annual Meeting of the Ecological Society of America, 1-6 August 2004, Portland, Oregon. Ecological Society of America, Washington, D. C.

Wilson, C. A, R. J. Mitchell, L. R. Boring, and J. J. Hendricks. 2002. Soil nitrogen dynamics in a fire-maintained forest ecosystem: results over a 3-year burn interval. Soil Biology and Biochemistry **34**: 679-698.

Table 1. Reports of excessive overstory longleaf pine mortality following re-introduction of fire into pine ecosystems after decades of fire suppression.

Federal Agencies

- USDA Forest Service
  - Ocala National Forest, FL [A]
  - Talladega National Forest, AL [B]
- US Fish and Wildlife Service
  - Mountain Longleaf National Wildlife Refuge, AL [B]
- Department of Defense
  - Eglin Air Force Base, FL [C]
  - Fort Gordon, GA [B]
  - Fort Jackson, SC [B]

State Agencies & Institutions

- Austin Cary Forest, FL [B]
- Autauga Demonstration Forest, AL [B, H]
- Florida Division of Forestry [B, D]
- Florida Fish and Wildlife Conservation Commission [C]
- Florida Park Service [E]
- Georgia Department of Natural Resources [C]
- North Carolina Division of Parks & Recreation [C]
- University of Florida [F]

NGO Land Management Agencies

- The Nature Conservancy
  - Alabama Chapter [C]
  - Florida Chapter [F]
  - Georgia Chapter [C]
  - Louisiana Chapter [G]

Forest Industry

- International Paper, Cantonment, FL [C]

A- Harold G. Shenk, personal communication, September 2001
B- Personal observations (JMV)
C- Varner and Kush 2004
D- Jim Meeker, personal communication, April 2001
E- Erik Johnson, personal communication, November 2003
F- Walt Thomson, personal communication, March 2003
G- Nelwin McInnis, personal communication, November 2000
H- John McGuire, unpublished data

List of Figures.

Figure 1a. A frequently-burned longleaf pine ecosystem reference condition at Eglin Air Force Base, Florida. Pristine pinelands are rare in current landscapes of the southeastern USA (D. Herring photograph).

Figure 1b. A typical long-unburned (37 years since fire) longleaf pine forest at the Ordway-Swisher Preserve, Florida. Many pinelands throughout the southeastern USA have undergone decades of fire suppression, leading to increases in the midstory, organic forest floor soil horizons, and decreases in plant and animal species richness (J.M. Varner photograph).

Figure 2. Forest floor development in a long-unburned (ca. 40 years since fire) longleaf pine forest at Eglin Air Force Base, Florida. In frequently-burned pinelands, only a thin Oi horizon forms; Oe and Oa horizons are signs of prolonged fire suppression. In many long-unburned pinelands organic soil accumulations surrounding large pines can exceed 25 cm in depth (J.M. Varner photograph).

Figure 3. Restoration fires in long-unburned longleaf pine forests damage canopy, stem, and root tissues often leading to excessive tree mortality. Flaming and smoldering fire can cause direct damage to canopy, stem, and root tissues. Pine mortality has been linked to smoldering combustion of duff near trees, perhaps caused by damage to root and/or stem tissues, or from indirect effects due to increased physiological stress.

Figure 1a

Figure 1b

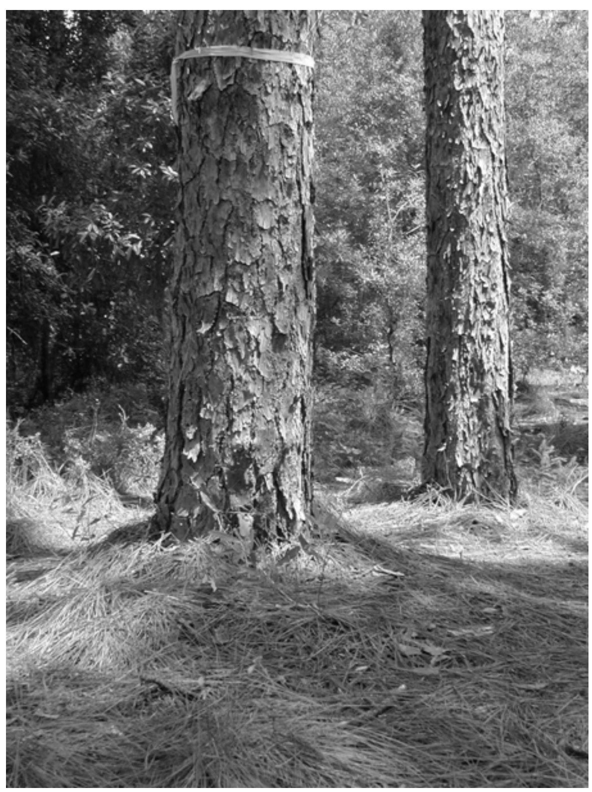


Figure 2

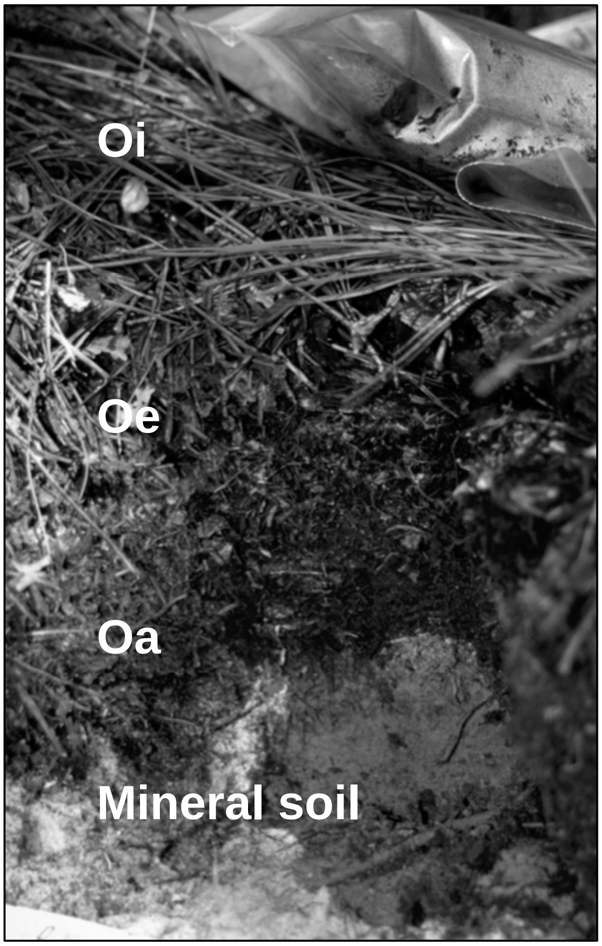
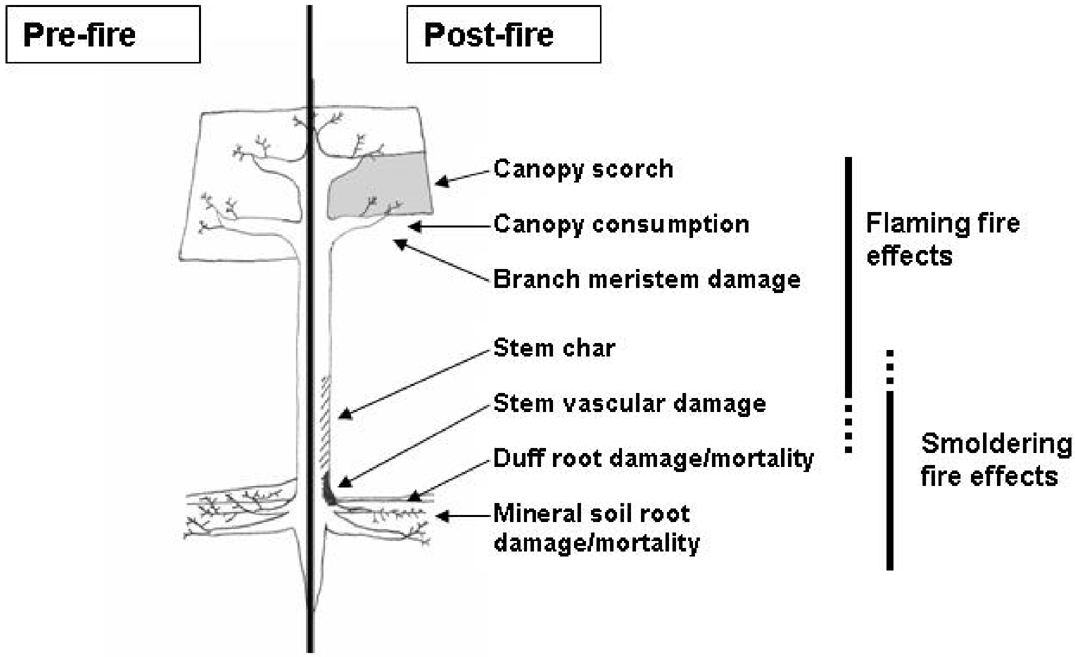


Figure 3


Pre-fire
Post-fire
Canopy scorch
Canopy consumption
Branch meristem damage
Stem char
Stem vascular damage
Duff root damage/mortality
Mineral soil root damage/mortality
Flaming fire effects
Smoldering fire effects

APPENDIX B.

Linking forest floor fuels with fire behavior and effects:
A review of our knowledge and research needs

J. Morgan Varner, III[1]
School of Natural Resources and Environment, University of Florida, Box 118526, Gainesville, FL 32611-8526, U.S.A.

[1]**Corresponding author and current address (e-mail: jmvarner@humboldt.edu)**
J. Morgan Varner, III
Department of Forestry and Watershed Management
Humboldt State University
1 Harpst Street
Arcata, CA 95521, U.S.A.
(707) 826-5622 Tel.
(707) 826-5634 Fax.

Abstract
Among the deleterious effects of fire exclusion in temperate coniferous forests is the accumulation of organic forest floor fuels. These organic forest fuels, particularly litter (Oi horizon) and duff (Oe and Oa horizons), influence fire behavior and effects. This review addresses the state of our knowledge on duff accumulation, the linkages between duff and fire effects, and primary research needs related to duff and fire-excluded temperate coniferous forests. Duff is primarily a smoldering fuel, subjecting basal vascular tissues and imbedded and underlying roots to lethal temperatures for hours to days following passage of the flaming front. Post-fire tree growth, stress, and mortality have been linked to duff smoldering throughout temperate coniferous forests. Relative to the benign emissions of flaming combustion, smoldering emissions generate noxious compounds and abundant greenhouse gases. Little is known regarding process-based duff accumulation and consumption patterns. Further work is needed on incorporating the complexity of forest floor and duff fuels into fire behavior and effects models. Given the continued large-scale exclusion of fire and its contribution to ecosystem fuel loading, fire behavior, and fire effects, future research should focus on a more holistic understanding of duff fuels, keys to restoration and management of fire-excluded temperate coniferous forests.

Keywords: ecological restoration, forest floor, fire effects, prescribed fire, smoldering duff

Introduction

Despite the fact that foresters and ecologists have recognized the role of fire in temperate coniferous forests for decades (e.g., Harper 1913, Chapman 1928, Stoddard 1931, Cooper 1960), fire exclusion is ongoing in many temperate savanna, woodland, and forest ecosystems. Excluding fire results in drastic alterations in ecosystems including: increased overstory density (Cooper 1960, Covington and Moore 1994, Gilliam and Platt 1999, Varner et al. 2000, Keane et al. 2002); altered overstory, midstory, and understory species composition (Heyward 1939, Gilliam and Platt 1999, Kush and Meldahl 2000, Varner et al. 2000, Keane et al. 2002, Provencher et al. 2003); degraded vertebrate habitat (Stoddard 1931, Leopold et al. 1963, Engstrom et al. 1984, Mushinsky 1985, Aresco and Guyer 1999); and, changes in the distribution and loading of surface and ground fuels (van Wagtendonk 1985, Swezy and Agee 1991, Haase and Sackett 1998, Stephens 2004, Varner et al. 2005). Among these changes resulting from fire exclusion, the development of deep organic matter accumulations on the surface of the mineral soil (hereafter, "forest floor") and the implications of this alteration on forests have received little attention.

In ecosystems maintained by frequent low-intensity fires, recently fallen litter is typically consumed by solid-phase combustion, interrupting decomposition into surface organic soil horizons (Oe and Oa, collectively termed "duff"). With successful fire suppression over the last century, many fire-prone temperate savannas, woodlands, and forests currently have well-developed duff horizons (Switzer et al. 1979, Swezy and Agee 1991, van Wagtendonk et al. 1998, Varner et al. 2000, Stephens et al. 2004, Varner et al. 2005, Hille and Stephens *In press*).

With re-introduction of fire, duff accumulations represent novel forest fuels that, in contrast to surface flaming combustion in “pristine” ecosystems, support smoldering combustion. Smoldering duff consumes active roots and concentrates long duration heating on basal meristematic tissues and surficial roots (Flinn and Wein 1977, Ryan and Frandsen 1991, Swezy and Agee 1991, Hungerford et al. 1995, Schimmel and Granstrom 1996, Haase and Sackett 1998, Dickinson and Johnson 2001). Smoldering duff fires kill trees, alter stand structure and species composition, and generate noxious smoke emissions (Ryan and Frandsen 1991, Swezy and Agee 1991, Hungerford et al. 1995, Varner et al. 2005).

Smoldering combustion has received relatively little attention in fire research (but see Frandsen 1987, Frandsen 1991, Frandsen 1997, Miyanishi 2001), even though smoldering fires are commonly associated with elevated fire severity (e.g., soil damage and plant mortality; Ryan and Frandsen 1991, Swezy and Agee 1991, Schimmel and Granstrom 1996). Downed woody debris (100-, 1000-, and 10,000-hour downed woody material) is often linked to smoldering and localized fire severity (Ottmar and Sandberg 1985, Brown et al. 1991, Ottmar et al. 1993, Costa and Sandberg 2004). If forest floor accumulations surrounding trees (“basal accumulations”; Sandberg et al. 2001) ignite, they typically smolder for long periods and are a major cause of post-fire conifer mortality (Swezy and Agee 1991, Ryan and Frandsen 1991, Hungerford 1995, Haase and Sackett 1998). Deep forest floor accumulations smolder for long periods (Covington and Sackett 1984, Swezy and Agee 1991, Hungerford et al. 1991, Haase and Sackett 1998, Miyanishi 2001, Varner et al., unpublished data), raising soil temperatures (Haase and Sackett 1998), damaging surficial tree roots (Swezy and Agee 1991) and stem vascular cambia (Ryan and Frandsen 1991, Ryan 2000).

The objectives of this review were to review current understanding of forest floor fuels, including fuel accumulation, ignition, combustion, and role in fire effects on long-unburned ecosystems. Research interest in duff smoldering is increasing due to the mounting backlog of areas that have undergone decades of fire exclusion and the increasing emphasis on restoring these communities (Parsons et al. 1986, Landers et al. 1995, Covington et al. 1997, Varner et al. 2005). Particular subjects of interest were: spatial patterns of accumulation, physical and chemical composition of duff accumulations, determinants of ignition and combustion, and patterns in moisture retention.

Forest floor accumulation patterns

In many temperate coniferous forests, forest floor and duff are patchily distributed. In contrast to boreal forests (Miyanishi and Johnson 2002) and peat-dominated forested wetlands (Hungerford et al. 1995), duff in temperate coniferous forests tends to be patchy and usually highest near the base of source trees (Ryan and Frandsen 1991, Swezy and Agee 1991, Gordon and Varner 2002, Varner et al. 2005, Hille and Stephens *In press*). In long-unburned *Pinus palustris* stands in Florida, Gordon and Varner (2002) found that forest floor depths decreased rapidly away from pines, with depths decreasing from 20.4 cm near the stem to 16.1 and 11.9 cm at 100 and 200 cm from the bole, respectively (Figure 1).

Given the variation in fire effects associated with duff combustion, foresters and ecologists need a better understanding of the spatial pattern of forest floor accumulations. Many studies report localized smoldering near the base of conifers (Ryan and Frandsen 1991, Swezy and Agee 1991), with one or more isolated actively smoldering areas (ranging from ca. 1 to 100cm^3) rather than a unified smoldering front (Hungerford et al. 1995, Miyanishi 2001, Miyanishi and Johnson 2002). Among the proposed hypotheses for basal smoldering are its increased depth, bulk density, reduced moisture content, and composition of its diverse fuel particles. Duff smoldering has been linked to thermal cover provided by overlying Oi and Oe horizons (Miyanishi and Johnson 2002). Thicker forest floor insulates the underlying smoldering front, aiding with distillation and volatilization of adjacent fuel particles. Bulk density varies spatially, and this variation should modify burning behavior (Stephens et al. 2004). Moisture content also varies near trees, with decreased duff moisture content observed beneath canopies due to their role in the interception of precipitation (Miyanishi and Johnson 2002, Hille and Stephens *In press*) and perhaps, inhibition of dew formation (Miyanishi and Johnson 2002). Another potential cause of localized smoldering is that forest floor fuel composition varies spatially, with bark slough concentrated near stems and needle litter beneath the canopy (Gordon and Varner 2002; Figure 1).

A better understanding of the mechanisms of the patterns of forest floor accumulation in the absence of fire is needed. Duff accumulation may be linked to the resistance to decomposition of the high phenolic and suberin content of bark slough (Susott 1982, Rogers et al. 1986, van Wagtendonk et al. 1998) near conifers. Low C: N ratios in Oi and duff horizons and high remnant phenolics and minerals in the duff horizons limit decomposition (Berg et al. 1982, Lee et al. 1983, Gholz et al. 1985; Table 1)). Decomposition may be slowed beneath coniferous canopies, due to the reductions in moisture (Keane et al. 2002, Miyanishi and Johnson 2002, Hille and Stephens *In press*). Given the variation in contemporary fire regimes across forest types, we should be able to determine at least the correlates, if not pinpoint mechanisms and thresholds in the patterns of duff accumulation in temperate coniferous forests.

Forest floor composition

The forest floor fuel contains fuel particles with diverse characteristics that influence ignition, burning, and extinction characteristics of surface and ground fires. Forest floor fuels be subdivided into Oi, Oe, and Oa horizons and at finer scales, by their composition (chemically, moisture holding capacity) and structure (depth, particle size, and bulk density). Forest floor fuels are often treated as either “litter layers” or “litter and duff layers,” rarely for the complex strata and components that are typified in coniferous forest floor accumulations.

Litter (Oi) horizons contain recently fallen and only slightly decomposed necromass (Pritchett 1979). Oi horizons contain particles with large surface area:volume ratios and large air spaces (low bulk density) resulting in the Oi having wide fluctuations in moisture that are characteristic of 1-hour timelag surface fuels (Byram 1959, Nelson 2001, Stephens et al. 2004). Oi horizons also harbor fine woody debris, cones and cone fragments, some broadleaf litter, and coarse bark slough. Freshly fallen litter contain the highest extractive contents of the forest floor (Table 1) that either lower ignition thresholds or increase fire intensity of burning fuels. The low moisture contents, low bulk density, high volatile content, and high surface area:volume of Oi horizons support flaming combustion fronts with high intensity and short duration (Fonda et al. 1998, Fonda 2001). Considering both the potential fire intensity created by Oi fuels and the diversity of particles found in Oi, this are deserves additional study both at the mesocosm (e.g., Fonda 2001) and ecosystem scales.

With partial decomposition and an extended period without fire, an Oe (fermentation) horizon forms underneath the Oi. Oe horizons are absent in frequently burned coniferous forests; their presence is indicative of a prolonged fire-free interval. The Oe is typified by decomposed but recognizable plant parts, reduced air space, stable moisture contents, fungal hyphae, and a proliferation of fine roots (Pritchett 1979, Harvey et al. 1994). Decomposition decreases necromass particle size, structural integrity, and cellulose: lignin ratio (Table 1). Due to increased moisture content and smaller particle sizes, Oe behaves as a ground fuel, burning without regard to wind direction and at very slow rates, primarily by smoldering combustion (Byram 1959, Hungerford et al. 1995, Nelson 2001, Miyanishi 2001). In smoldering fires, Oe accumulations insulate and conceal underlying Oa smoldering. Of all the forest floor horizons, Oe is the most enigmatic; Oe fuels resist water loss, contain abundant roots and hyphae, and are tightly packed thereby resisting ignition from above and below.

With continued decomposition, an Oa (humus) horizon forms beneath the Oe and overlying the mineral soil surface in fire-excluded longleaf pine forests. In many temperate coniferous forests growing on acidic sandy soils, a mor humus or Lentar ectogranic layer is created (Heyward 1939, Mader 1953, Wilde 1966). As with decomposition to a fermentation horizon, particle sizes in the Oa are small litter structures not macroscopically recognizable, cellulose: lignin ratios are low, and air space is greatly reduced (van Wagtendonk et al. 1998, Stephens et al. 2004). Mineral ash content in Oa is high due to both the admixture of mineral soil from the underlying mineral horizon and as remnant products from decomposition (van Wagetendonk et al. 1998). The Oa horizon consists of fine organic matter and considerable tree root proliferation (Pritchett 1979, Harvey et al. 1994). Oa horizons are subjected to drying from the underlying mineral soil, so they are often drier than the overlying Oe (Nelson 2001, Varner, unpublished data). As with Oe, the Oa behaves as a ground fuel (Byram 1959, Hungerford et al. 1995, Nelson 2001, Miyanishi 2001) and its presence is an indicator of prolonged periods of fire exclusion. Oe and Oa horizons, collectively termed “duff,” are often treated together in fire management and research. The two horizons, however, retain and gain moisture, ignite and burn differently. Given the contrast between the two horizons, the use of “duff” as a homogenous stratum may be an oversimplification of complex strata.

The composition of basal forest floor accumulations is spatially variable (Gordon and Varner 2002, Figure 1). The variation in forest floor composition is likely critical to fire behavior, with the ignition, combustion, and smoldering of these contrasting parts varying widely (Miyanishi 2001). In many boreal and temperate peat forests, duff is treated as a relatively homogeneous fuel. Indeed, commercial peat has been used as a standard to test for effects and determinants of ignition, combustion, and effects on soil heating (Frandsen 1987, Hungerford et al. 1995, Miyanishi and Johnson 2002). In fact, temperate coniferous forest floor fuels are complex, containing fuel particles with contrasting combustion characteristics. The combustion of forest floor fuels ranges from short-duration needle litter (Fonda et al. 1998, Fonda 2001) to long-duration cones (Fonda and Varner 2005) and woody material (Costa and Sandberg 2004). Accumulations nearest to many thick-barked conifers contain a large proportion of bark slough. Bark of many conifers contains high temperature suberin and lignin compounds that are difficult to ignite, but burn with great intensity (Susott 1982, Rogers et al. 1986). Basal accumulations in a long-unburned *Pinus palustris* stand in Florida were dominated by bark slough (Gordon and Varner 2002) and other forests have similar patterns (R. Ottmar, *unpublished data*). Conifer cones are also clumped around individual trees and likely serve as localized sources of both high intensity and long duration combustion (Fonda and Varner 2005). Hille and Stephens (*In press*) provide the only known data on spatial variability of forest floor fuels. No work exists to date that incorporates the variability in fuel depth, structure, and composition; this represents a major oversight in our understanding of fire effects in fire-excluded forests.

While forest floor fuels are not as simple as previously assumed, they are surely neither as complex as presented here. A determination of the relative importance of fuel composition and structure on forest floor ignition and combustion is needed. This determination could be accomplished in laboratory mesocosms with contrasting fuelbeds or perhaps in an ordination framework using more elaborate pre-fire data in field burning conditions. Developing a process-based model incorporating fuel heterogeneity may help elucidate future research directions.

Controls of duff moisture content

Moisture content is the primary determinant of ignition and combustion of forest floor and duff fuels (Sandberg 1980, Frandsen 1987, Frandsen 1991, Hungerford et al. 1995, Miyanishi 2001). To date, we have compiled examples of empirical (Anderson et al. 2003) and process-based (Miyanishi 2001, Miyanishi and Johnson 2002) models of duff moisture variation. Both of these approaches, however, suffer from either a site-specific applicability or from using assumptions based on simplistic models of duff. The prior weakness can be addressed on a site-specific basis and its limits are well-understood (Miyanishi 2001, Miyanishi and Johnson 2002). The treatment of duff as a simplistic fuel, however, is a shortcoming of our current understanding. Contrary to current models, duff fuels are structurally and compositionally complex (see above), are located above and below dynamic adsorptive surfaces (Oi and Oe above; mineral soil below) and contain active living roots and mycorrhizae (Harvey et al. 1994, Gordon and Varner 2002). Root and mycorrhizal activity within Oe and Oa duff not only serve to drain these fuels of moisture, but may also be responsible for substantial wetting in response to hydraulic lift of subsurface moisture by conifers (Dawson 1993, Horton and Hart 1998, Espeleta et al. 2004). To what degree the latter is responsible for localized increases in moisture is yet to be determined, but the influence of active root uptake will surely affect forest floor moisture dynamics. Future work on the effects of elevated temperature on duff roots and mycorrhizae is warranted.

Given our understanding of thresholds of duff ignition (Sandberg 1980, Frandsen 1987, Frandsen 1991, Frandsen 1991), many questions regarding duff ignition and combustion remain unanswered. In restoration burning in *Pinus ponderosa* forests in southern Oregon, Agee and collaborators (Swezy and Agee 1991, Agee 2003) observed abundant duff smoldering beyond threshold moisture contents. Similar observations have been recorded in large field studies (Chapter 2) and in small single tree fires (personal observation, Flamelot Hammock, March 2002). Mechanisms for wet duff ignition may be linked to the presence of dry duff vectors such as 10-hr woody timelag fuels and downed cones common in long-unburned stands. Small timelag fuels dry much faster than underlying duff and burn for long periods, preheating and igniting underlying duff. Similarly, cone fuels have very low field moisture contents (contents lower than litter in longleaf pine sites, Varner, *unpublished data*) and burn with both high intensity (maximum flame lengths of individual *Pinus palustris* cones at field moisture contents averaged 87.1 cm) and long duration (individual cones burned for an average of 52.8 min; Fonda and Varner 2005) that facilitates duff pre-heating and ignition. Given that we have a poor grasp on vector moisture dynamics and the mechanisms of duff ignition, significant work is needed on the subject of vectors of duff ignition.

Field observations and empirical data (Brown et al. 1991, Fonda and Varner 2005) suggest that downed woody debris and pine cones serve as vectors of ignition to underlying duff horizons. Both types of material are noted long-duration fuels (Taylor and Fonda 1990, Costa and Sandberg 2004, Fonda and Varner 2005) that contribute proportionately more to fire behavior than is suggested by their relatively minor contribution to the mass or volume of the fuelbed. The dominance of sloughed bark in basal accumulations may be important in patterns of fire behavior. While bark is difficult to ignite, it contains high temperature volatiles attributed to suberin (Rogers et al. 1986). The concentrations of bark slough and the presence of downed woody and cone fuels may explain the observed smolder “cavities” surrounding trees subjected to long-duration duff fires.

Conclusions

Forest floor fuels are an often overlooked component of fuel loading, and basal accumulations even more so. Given the proximity of basal accumulations of duff to heat-sensitive tree tissues, understanding the implications of changes in these fuels is critical to understanding the mechanisms and severity of fire effects. The effects of fire exclusion obviously have far-reaching effects on forests beyond changing stand structure, species composition, and habitat availability (Keane et al. 2002, Varner et al. 2005). Incorporation of a greater understanding of fire exclusion on fuels, fire behavior, and fire effects will invigorate our ability to restore and manage changing ecosystems.

Acknowledgments

This project was supported by funds provided to the USDA Forest Service, Southern Research Station, Asheville, North Carolina, from the Joint Fire Science Program of the Departments of Agriculture (Forest Service) and Interior (Bureau of Land Management) and supplementary support from the University of Florida School of Natural Resources and Environment, The Nature Conservancy, Eglin Air Force Base Jackson Guard, and Humboldt State University. Helpful comments and encouragement were provided by F.E. Putz, D. Gordon, K. Hiers, R. Fonda, R. Ottmar, A. Long, R. Mitchell, and T. Martin.

List of References

Agee, J. K. 2003. Monitoring post-fire mortality in mixed-conifer forests of Crater Lake, Oregon. Natural Areas Journal 23:114-120.

Aresco, M. J. and C. Guyer. 1999. Burrow abandonment by gopher tortoises in slash pine plantations of the Conecuh National Forest. Journal of Wildlife Management 63:26-35.

Berg, B., K. Hannus, T. Popoff, and O. Theander. 1982. Changes in organic chemical components of needle litter during decomposition. Long-term decomposition in a Scots pine forest. Canadian J. Botany 60: 1310-1319.

Brown, J. K., E. D. Reinhardt, W.C. Fischer. 1991. Predicting duff and woody fuel consumption in northern Idaho prescribed fires. Forest Science 37: 1550-1566.

Chapman, H. H. 1932. Is the longleaf type a climax? Ecology 13(4): 328-34.

Costa, F., and D. Sandberg. 2004. Mathematical model of a smoldering log. Combustion and Flame 139: 227-238.

Covington, W.W., and S.S. Sackett. 1984. The effect of a prescribed burn southwestern ponderosa pine on organic matter and nutrients in woody debris and forest floor. Forest Science 30:183-192.

Covington, W.W., P.Z. Fulé, M.M. Moore, S.C. Hart, T.E. Kolb, J.N. Mast, S.S. Sackett, and M.R. Wagner. 1997. Restoration of ecosystem health in southwestern ponderosa pine forests. Journal of Forestry 95:23-29.

Dawson, T.E. 1993. Hydraulic lift and water use by plants: implications for water balance, performance and plant-plant interactions. Oecologia 95: 565-574.

Dickinson, M. B. and E. A Johnson. 2001. Fire effects on trees. Pages 477-525 *in*: Johnson, E. A. and K. Miyanishi, Eds. Forest Fires. Academic Press, New York.

Engstrom, R. T., R. L. Crawford, and W. W. Baker. 1984. Breeding bird populations in relation to changing forest structure following fire exclusion: a 15-year study. The Wilson Bulletin 96: 437-50.

Espeleta, J.F., J.B. West, and L.A. Donovan. 2004. Species-specific patterns of hydraulic lift in co-occurring adult trees and grasses in a sandhill community. Oecologia 138: 341-349.

Ferguson, S. A. J.E. Ruthford, S.J. McKay, D. Wright, C. Wright, and R. Ottmar. 2002. Measuring moisture dynamics to predict fire severity in longleaf pine forests. Int. J. of Wildland Fire 11: 267-279.

Flinn, M.A. and R.W. Wein. 1977. Depth of underground plant organs and theoretical survival during fire. Canadian J. Botany. 55: 2550-2554.

Fonda, R.W., L.A. Belanger, and L.L. Burley. 1998. Burning characteristics of western conifer needles. Northwest Science 72:1-9.

Fonda, R.W. 2001. Burning characteristics of needles from eight pine species. Forest Science 47:390-396.

Fonda, R.W. and J.M. Varner. 2005. Burning characteristics of cones from eight pine species. Northwest Science 78: 322-333.

Frandsen, W. H. 1987. The influence of moisture and mineral soil on the combustion limits of smoldering forest duff. Canadian Journal of Forest Research 17: 1540-1544.

Frandsen, W. H. 1991. Burning rate of smoldering peat. Northwest Science 65: 166-172.

Frandsen, W. H. 1997. Ignition probability of organic soils. Canadian Journal of Forest Research 27: 1471-1477.

Frandsen, W. H. and K. C. Ryan. 1985. Soil moisture reduces heat flux and soil temperatures under a burning fuel

pile. Canadian Journal of Forest Research 16: 244-248.
Gholz, H.L., C.S. Perry, W.P.J. Cropper, and L.C. Hendry. 1985. Litterfall, decomposition, and nitrogen and phosphorus dynamics in a chronosequence of slash pine (*P. elliottii*) plantations. Forest Science 31: 463-78.
Gilliam, F. S. and W. J. Platt. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. Plant Ecology 140:15-26.
Gordon, D.R. and J.M. Varner. 2002. Old growth longleaf pine restoration and management. Final Report to Eglin Air Force Base Jackson Guard, Niceville, Florida. 33 p. The Nature Conservancy, Altamonte Springs, Florida.
Haase, S.M. and S.S. Sackett. 1998. Effects of prescribed fire in giant sequoia-mixed conifer stands in Sequoia and Kings Canyon National Parks. Tall Timbers Fire Ecology Conference Proceedings 20: 236-243.
Harper,R.M. 1913. Economic botany of Alabama. Monograph No. 8. Geological Survey of Alabama, Montgomery, AL.
Harvey, A.E., Geist, J. M.., McDonald, G.L., Jurgensen, M. F., Cochran, P. H., Zabowski, D., and R.T. Meurisse 1994. Biotic and abiotic processes in eastside ecosystems: the effects of management on soil properties, processes, and productivity. Gen. Tech. Rep. PNW-GTR-323. USDA Forest Service, Pacific Northwest Research Station, Portland, OR.
Heyward, F. 1938. Soil temperatures during forest fires in the longleaf pine region. Journal of Forestry 36: 478-491.
Heyward, F. 1939. The relation of fire to stand composition of longleaf pine forests. Ecology 20: 287-304.
Hille, M.G. and S.L. Stephens. Mixed conifer forest duff consumption during prescribed fires: Tree crown impacts. Forest Science. *In press*.
Horton, J.L., and S.C. Hart. 1998. Hydraulic lift: a potentially important ecosystem process. Trends in Ecology and Evolution 13(6):232-235.
Hough, W.A. 1982. Phytomass and nutrients in the understory and forest floor of slash/longleaf pine stands. Forest Science 28: 359-72.
Hungerford, R. D., W. H. Frandsen, and K. C. Ryan. 1995. Ignition and burning characteristics of organic soils. Tall Timbers Fire Ecology Conference Proceedings 19: 78-91. Tall Timbers Research Station, Tallahassee, FL.
Keane, R.E., K.C. Ryan, T.T. Veblen, C.D. Allen, J. Logan, and B. Hawkes. 2002. Cascading effects of fire exclusion in Rocky Mountain ecosystems: A literature review. Gen. Tech. Rep. RMRS-GTR-91. Fort Collins, CO: U.S. Department of Agriculture, Forest Service Rocky Mountain Research Station. 24p.
Kush, J. S. and R. S. Meldahl. 2000. Composition of a virgin longleaf pine stand in south Alabama. Castanea 65: 56-63.
Lee, R.S., W.L. Pritchett, and W.H. Smith. 1983. Forest floor characteristics under longleaf-slash pine on two Spodosols. Forest Ecology and Management 5: 193-205.
Leopold, A. S., S. A. Cain, C. M. Cottam, I. N. Gabrielson, and T. L. Kimball. 1963. Wildlife management in the national parks. Transactions of the North American Wildlife and Natural Resources Conference 28: 29-44.
Mader, D.L. 1953. Physical and chemical characteristics of the major types of forest humus found in the United States and Canada. Soil Science Soc. Proc. 155-159.
McHugh, C. W. and T. E. Kolb. 2003. Ponderosa pine mortality following fire in northern Arizona. International Journal of Wildland Fire **12:**1-16.
McMahon, C. K. 1983. Characteristics of forest fuels, fire and emissions. Paper No. 45.1 in: Proceedings of the 76th Annual Meeting of the Air Pollution Control Association, 19-24 June 1983, Atlanta, Georgia. Air Pollution Control Association, Pittsburgh, Pennsylvania. 24 p.
McMahon, C. K., D. D. Wade, and S. N. Tsouklas. 1980. Combustion characteristics and emissions from burning organic soils. Paper No. 15.5 in: Proceedings of the 73th Annual Meeting of the Air Pollution Control Association, 22 -27 June 1980, Montreal, Quebec. Air Pollution Control Association, Pittsburgh, Pennsylvania. 17 p.
Miyanishi, K. 2001. Duff consumption. Pages 437-475 *in*: Johnson, E. A. and K. Miyanishi, Eds. Forest Fires. Academic Press, New York.
Miyanishi, K. and E.A. Johnson. 2002. Process and patterns of duff consumption in the mixedwood boreal forest. Can. J. Forest Res. 32: 1285-1295.
Mushinsky, H.R. 1985. Fire and the Florida sandhill herpetofaunal community: with special attention to the responses of *Cnemidophorus sexlineatus*. Herpetologica 4: 333-342.
Nelson, R. M. 2001. Water relations of forest fuels. Pages 79-149 in Johnson, E. A. and K. Miyanishi, eds. Forest Fires. Academic Press, New York.
Ottmar, R.D. and D.V. Sandberg. 1985. Calculating moisture content of 1000-hour timelag fuel in western Washington and western Oregon. Res Pap PNW-336. USDA Forest Service, PNW Res. Sta. Portland, OR. 16 p.

Ottmar, R.D. and R.E. Vihnanek. 2000. Stereo photo series for quantifying natural fuels. Volume VI: longleaf pine, pocosin, and marshgrass types in the Southeast United States. PMS 835. Boise, ID: National Wildfire Coordinating Group, National Interagency Fire Center. 56 p.

Ottmar, R.D., R.E. Vihnanek, and J. W. Mathey. 2003. Stereo photo series for quantifying natural fuels. Volume VIA: sand hill, sand pine scrub, and hardwoods with white pine types in the Southeast United States with supplemental sites for volume VI. PMS 838. Boise, ID: National Wildfire Coordinating Group, National Interagency Fire Center. 78 p.

Parsons, D. J., D. M. Graber, J. K. Agee, and J. W. van Wagtendonk. 1986. Natural fire management in national parks. Environmental Management 10(1): 21-4.

Pritchett, W. L. 1979. Properties and Management of Forest Soils. Wiley, New York. 500 p.

Provencher, L., A.R. Litt, and D.R. Gordon. 2003. Predictors of species richness in northwest Florida longleaf pine sandhills. Conservation Biology 17: 1660-1671.

Rogers, J. M., R. A. Susott, and R. G. Kelsey. 1986. Chemical composition of forest fuels affecting their thermal behavior. Canadian Journal of Forest Research 16: 721-726.

Ryan, K. C. and W. H. Frandsen. 1991. Basal injury from smoldering fires in mature *Pinus ponderosa* Laws. International Journal of Wildland Fire 1:107-118.

Sandberg, D.V. 1980. Duff reduction by prescribed underburning in Douglas-fir. USDA For. Serv. Res. Pap. PNW-RP-272. 18 p.

Sandberg, D.V., R. D. Ottmar, and G.H. Cushon. 2001. Characterizing fuels in the 21st century. International Journal of Wildland Fire 10: 381-387.

Schimmel, J. and A.Granstrom. 1996. Fire severity and vegetation response in the boreal Swedish forest. Ecology 77: 1436-1450.

Stephens, S.L. and M.A. Finney. 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. Forest Ecology and Management 162: 261-271.

Stephens, S.L. 2004. Fuel loads, snag abundance, and snag recruitment in an unmanaged Jeffrey pine-mixed conifer forest in Northwestern Mexico. Forest Ecology and Management 199: 103-113.

Stephens, S.L., Finney, M.A., and Schantz, H. 2004. Bulk density and fuel loads of ponderosa pine and white fir forest floors: impacts of leaf morphology. Northwest Science 78: 93-100.

Stoddard,H.L., Sr. 1931. The Bobwhite Quail: Its habits, preservation and increase. Charles Scribner's Sons, New York, NY.

Stott, P. 2000. Combustion in tropical biomass fires: a critical review. Progress in Physical Geography 24: 355-377.

Susott, R. A. 1982. Characterization of the thermal properties of forest fuels by combustible gas analysis. Forest Science 28: 404-420.

Swezy, D.M. and J.K. Agee. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Canadian Journal of Forest Research 21: 626-634.

Switzer, G. L., M. G. Shelton, and L. E. Nelson. 1979. Successional development of the forest floor and soil surface on upland sites of the east Gulf Coastal Plain. Ecology 60: 1162-1171.

Taylor, K.L. and R.W. Fonda. 1990. Woody fuel structure and fire in subalpine fir forests, Olympic National Park, Washington. Canadian Journal of Forest Research 20: 193-199.

van Wagtendonk, J.W. 1985. Fire suppression effects on fuels and succession in short-fire-interval wilderness ecosystems. Pages 119-126 in: Lotan, J.E., B.M. Kilgore, W.C. Fischer, and R.W. Mutch. Proceedings of a symposium and workshop on wilderness fire. Gen. Tech. Rep. INT-182. USDA Forest Service Int. Res. Station.

van Wagtendonk, J.W., W.M. Sydoriak, and J.M. Benedict. 1998. Heat content variation in Sierra Nevada conifers. International Journal of Wildland Fire 8: 147-158.

Varner, J. M., J. S. Kush, and R. S. Meldahl. 2000. Ecological restoration of an old-growth longleaf pine stand utilizing prescribed fire. Tall Timbers Fire Ecology Conference Proceedings 21: 216-219. Tall Timbers Research Station, Tallahassee, FL.

Varner, J.M. and J.S. Kush. 2004. Old-growth longleaf pine forests and savannas of the southeastern USA: Status and trends. Natural Areas Journal 24:141-149.

Varner, J.M., D.R. Gordon, F.E. Putz, and J.K. Hiers. 2005. Novel fire effects in southeastern pine forests: smoldering fire and overstory pine mortality. Restoration Ecology 13:1-9.

Wilde, S.A. 1966. A new systematic terminology of forest humus layers. Soil Science 101:403-407.

Figure 1. Basal forest floor depths and composition in a long-unburned longleaf pine forest in northern Florida, USA.

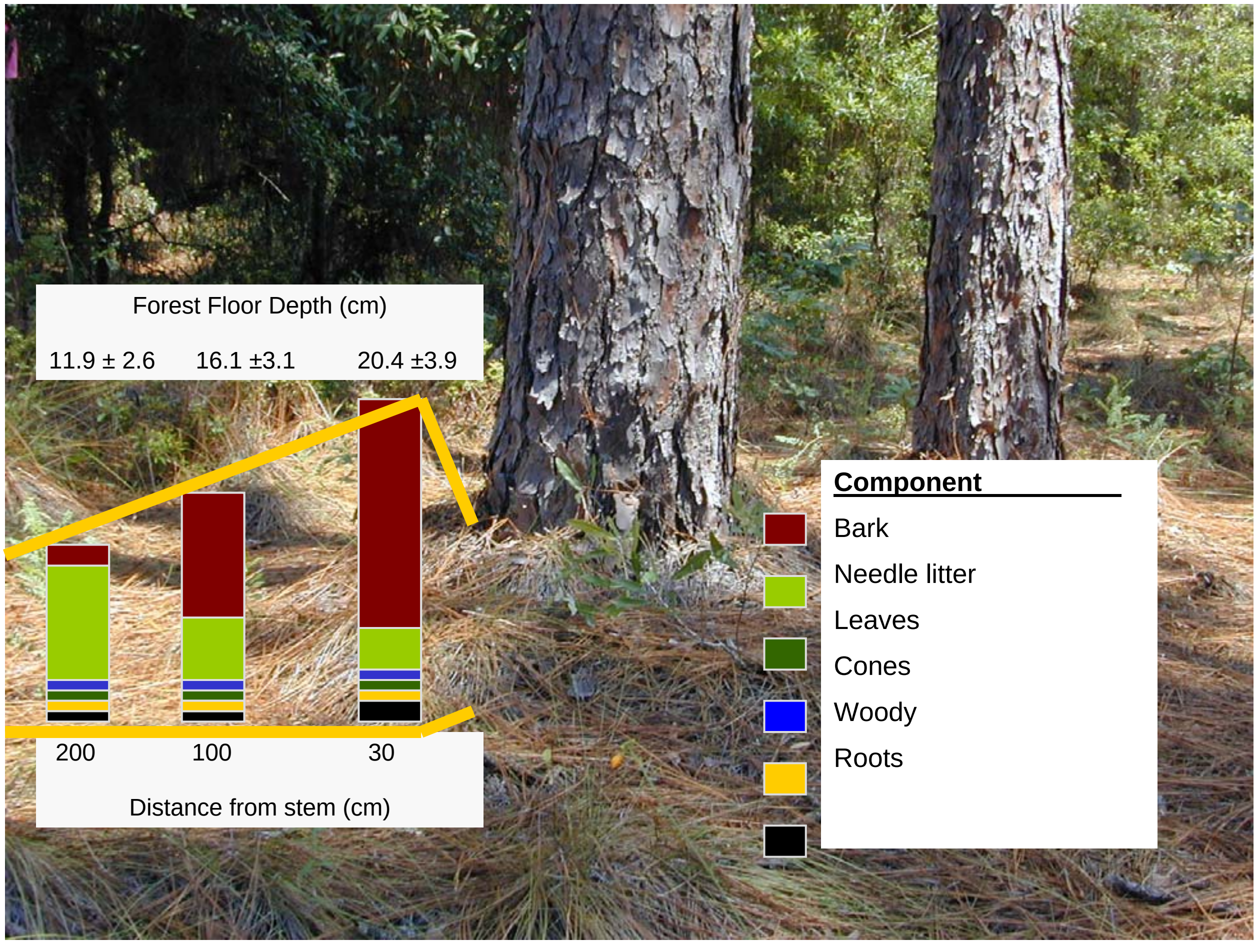


Figure 2. Smoldering in long-unburned coniferous forests is typically patchy, with smolder cavities (A) located near the bole. The lower image is a thermal infrared image of a smoldering longleaf pine 110 min after ignition, illustrating the localized heating that occurs in duff fires (image courtesy of J. O'Brien, USDA Forest Service Southern Research Station).

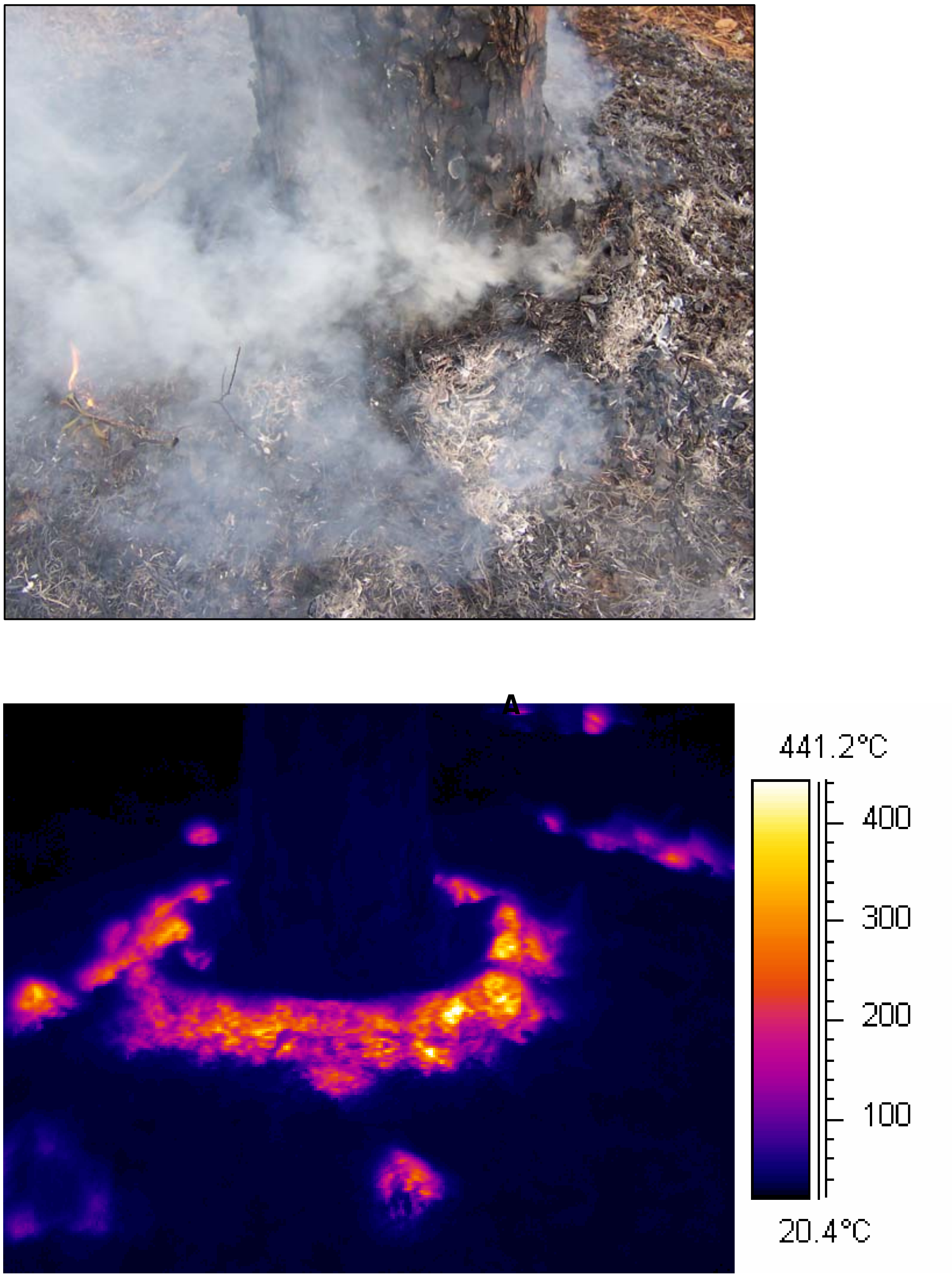


Table 1. Carbon fractions from basal fuel accumulations in a long-unburned longleaf pine forest floor at Smith Lake, Ordway-Swisher Preserve, Florida, USA.

		Mean Percent of Sample								
Forest Floor Component	*N*	Extractives	Hemicellulose		Cellulose		Lignin		Ash	
Litter (Oi horizon)	5	28.4	13.3	*B*[1]	31.3	*B*	26.3	*A*	0.6	*B*
Fermentation (Oe)	5	28.2	11.6	*B*	28.1	*B*	31.5	*B*	0.6	*B*
Humus (Oa)	5	29.6	6.3	*A*	21.5	*A*	35.4	*B*	7.2	*A*
Intact bark	5	26.0	6.7		28.7		38.0		0.5	
Sloughed bark	5	30.9	6.2		28.6		33.9		0.5	
Recently fallen cones	5	18.9[2]	15.4		34.6		30.7		0.4	
Weathered cones	5	22.7	8.3		28.3		38.6		2.0	

[1] Percentages followed by different letters denote significant differences (P < .05) among forest floor components determined using post-hoc Tukey's HSD.
[2] Percentages underlined denote significant differences (P < .05) determined using paired *t*-tests.

APPENDIX C.

Modeled versus observed fire effects in long-unburned *Pinus palustris* forests

J. Morgan Varner, III,[1, 2] School of Natural Resources and Environment, University of Florida, Box 118526, Gainesville, FL 32611-8526, U.S.A.
J. Kevin Hiers, The Nature Conservancy of Georgia, Thomasville, GA 31792, U.S.A.
Doria R. Gordon, The Nature Conservancy, Box 118526, Gainesville, FL 32611-8526, U.S.A.
Francis E. Putz, Department of Botany, University of Florida, Box 118526, Gainesville, FL 32611-8526, U.S.A.

[1]**Corresponding author (e-mail: jmvarner@humboldt.edu)**
J. Morgan Varner, III
Department of Forestry and Watershed Management
Humboldt State University
1 Harpst Street
Arcata, CA 95521, U.S.A.
(707) 826-5622 Tel.
(707) 826-5634 Fax.

[2] Present address: Department of Forestry and Watershed Management, Humboldt State University, 1 Harpst Street, Arcata, CA 95521 Email: jmvarner@humboldt.edu

Introduction

The effects of fire exclusion on temperate coniferous forests have important implications for reintroduction of fire and wildfire. In most historically fire-maintained temperate coniferous forests, fuel loads were maintained at low levels, often with no forest floor development or coarse woody debris retention (Agee 2002, Stephens 2004, Varner et al. 2005). With widespread fire exclusion in many temperate coniferous forests, fuels have accumulated, leading to uncharacteristic fuel loads (van Wagtendonk 1985, Keane et al. 2002) that smolder for long periods following ignition, heating both stems and root vascular tissues. What results from these smoldering fires is heavy tree mortality (Ryan and Frandsen 1991, Swezy and Agee 1991, Haase and Sackett 1998, Varner et al. 2000, Stephens and Finney 2002, Agee 2003, McHugh and Kolb 2003, Varner et al. 2005), uncharacteristic of these normally fire-resistant conifers.

Researchers and fire managers commonly use simulations models to predict effects of fire or fuels and silvicultural treatments (Stephens 1998, Brose and Wade 2002, Agee 2003). Since prescribed fire is often expensive, operationally demanding, and unforgiving, these models have great utility. Among other models (e.g., BehavePlus, Andrews and Bevins 2003; CONSUME, Ottmar et al. 1993; FARSITE, Finney 1998), fire effects predictive models (NEXUS, Scott 1999; FOFEM, Reinhardt 2003) have great utility for planning prescribed and wildland fire use fires, as well as determining post-wildfire priorities.

The need for reintroduction of fire is mounting throughout North American forests (e.g., van Wagtendonk 1985, Covington et al. 1997), particularly in southeastern *Pinus palustris* (longleaf pine) ecosystems (Hermann 1993, Landers et al. 1995). Fire exclusion in longleaf pine ecosystems leads to decreased plant and animal species richness (Heyward 1939, Engstrom et al. 1984, Mushinsky 1985, Aresco and Guyer 1999, Gilliam and Platt 1999, Kush and Meldahl 2000, Provencher et al. 2003, Varner et al. 2005), increased overstory density (Gilliam and Platt 1999, Varner et al. 2000), and heavy accumulations of forest floor material (Varner et al. 2005). Restoring fire to long-unburned longleaf pine forests has been surprisingly problematic; among the negative outcomes including excessive long-duration smoke emissions and weedy species proliferation, large-scale overstory pine mortality looms large. Examples of heavy post-restoration mortality are abundant across the region (Varner and Kush 2004, Varner et al. 2005).

The objectives of this study were to compare predicted fire effects to empirical results in large landscape fires and small individual tree burning in long-unburned longleaf pine forests. The prediction was that current models developed for pristine ecosystems would perform poorly when compared with previously, but now more common, forests. FOFEM 5.2.1, a common tool for fire and restoration managers (e.g., Agee 2003, Reinhardt 2003), was selected for analysis using inputs from field burns in an on-going project. Specific hypotheses were:

1. mortality estimates would be poor in fire excluded stands, since second-order effects dominate these fires;
2. estimates of fuel consumption, since based on physical models, would model well in fire excluded stands; and,
3. estimates of soil heating, since the product of uncharacteristic changes due to fire exclusion, would be underestimated by current model output.

These results can assist restorationists and managers in longleaf pine ecosystems, but should also help identify patterns that may hold in other fire-excluded forests. This work is important for evaluating the utility of current predictive models and to elucidate improvements to invigorate these important decision-support tools.

Methods

Study Sites

Empirical data were gathered from experimental fires at both stand- and individual tree scales. Large operational prescribed fires were ignited in two long-unburned sites dominated by *Pinus palustris* at Eglin Air Force Base in Okaloosa County, Florida (N 30° 38', W 86° 24'; Figure 1). Both stands were dominated by a remnant canopy of longleaf pine (45-200 trees > 10 cm DBH ha^{-1}), sand pine (*Pinus clausa* var. *immuginata*), turkey oak (*Quercus laevis*), sand live oak (*Q. geminata*), sand post oak (*Q. margaretta*), with a woody midstory dominated by yaupon holly (*Ilex vomitoria*) and littlehip hawthorn (*Crataegus spathulata*) and scattered laurel oaks (*Q. hemisphaerica*) with little herbaceous species cover (Gordon and Varner 2002). Soils at both sites are deep, excessively well-drained coated Typic Quartzipsamments of the Lakeland series with mean depth to water table exceeding 200 cm. Slopes are gentle (0 to 5%) and elevations range between 50 and 60 m above msl (Overing et al. 1995). The climate of the area is subtropical, characterized by warm, humid summers and mild winters, with mean temperatures of 25° C and mean annual precipitation of 1580 mm, most of which falls from June to September (Overing et al. 1995).

Stands at each of the two sites were randomly assigned to one of three burning treatments based on day-of-burn duff moisture content (dmc; percent of dry weight): dry (60% dmc); moist (90% dmc); and wet (120% dmc). For each experimental fire, fire weather, fuel moisture, and fire behavior were recorded (Table 1). All prescribed burns were ignited during the spring, from late February to April. To minimize variation in fire behavior, all fires were ignited using strip head fires or spot-grid ignition (Wade and Lunsford 1989), with ignition patterns adjusted to minimize variation in flame lengths and rate of spread.

Individual tree fires were used to determine localized soil heating, measures that are different to obtain in large operational fires. Since smoldering fires are small, behave in response to small-scale control, and propagate slowly in duff fuels, these small fires mimic the patterns of large fires. The individual tree site was located near Smith Lake within the Katharine Ordway Preserve-Carl Swisher Memorial Sanctuary (hereafter, "Ordway") in Putnam County, Florida (N 29º 40', W 81º 74; Figure 1). The Smith Lake Tract is dominated by a canopy of longleaf pine, turkey oak, sand live oak, laurel oak, and a remnant understory of southern wiregrass (*Aristida stricta*) with patches of Florida rosemary (*Ceratiola ericoides*), all typical of fire-suppressed north Florida sandhills. Soils of the site are deep, extensively well-drained hyperthermic, uncoated Lamellic Quartzipsamments of the Candler series (Readle 1990). The topography is gentle, with gentle north-facing slopes < 5% and elevations averaging 16 m above msl.

Individual tree fires at Ordway were ignited in 1 m radius plots surrounding 16 randomly selected mature (30 – 50 cm DBH) individual pines. Three treatments were installed that subjected pines to root, stem, or both root and stem heating. In all burns, duff and mineral soil temperatures were measured using Type J (range 0º to 1200° C) thermocouples connected to a Campbell Scientific CR10X datalogger. Temperature was measured at three points 120º apart in the lower duff (Oa horizon; 3 points), and directly beneath these points in the mineral soil at 5, 10, and 20 cm depths (9 points). Maximum temperature was recorded every two minutes at all points from 15 minutes prior to ignition through the duration of the burning day (termination was required by 1700 hours on all but one of the burning days).

Simulation Modeling

To model fire effects, we used the First-Order Fire Effects Model (FOFEM 5.2.1; Reinhardt 2003). FOFEM simulates smoke products (CO, CO_2, CH_4, NO_X, SO_2, $PM_{2.5}$, PM_{10}), soil heating depth, fuel consumption (by timelag category and forest floor horizon), and overstory tree mortality. A combination of collected field data and loadings from local samplings (Ottmar and Vihnanek 2000, Ottmar et al. 2003; Table 1) for user-defined inputs for fuel moisture and fuel loadings were used. For fuel model input, SAF cover type 70 (longleaf pine; Eyre 1980) with 15 year rough (the maximum period possible) was used, appropriate for the xeric longleaf pine forests at both sites. Flame height inputs into FOFEM were derived from observations in field prescribed fires.

Results

Simulated mortality estimates for the long-unburned longleaf pine stands were lower than field estimates under all burning conditions. FOFEM predicted 35 % overstory mortality across all moisture scenarios (Table 2). In field burns, there was no overstory pine mortality during the first year following burns; during the second year, mortality was 0.5, 3.0, and 20.5 % in the wet, moist, and dry scenarios, respectively (Table 2). In simulations of all moisture scenarios, probability of tree mortality decreased with increasing tree diameter (Table 2). In observed field burns, mortality probabilities were uniform in wet burns, concentrated in smaller trees in moist burns, and concentrated in larger pines in dry burns (Table 2).

Duff consumption and smoldering times were greater in field burns that in simulations (Table 2). FOFEM predicted no duff consumption in the wet and moist burns, and only 8.1% in the dry scenario. Field burns resulted in duff consumption across all moisture scenarios; duff consumption in wet burns averaged 5.0%, in moist 14.5, and 46.5 in the dry burns (Table 2). Similarly, FOFEM predicted short smoldering times (6.8, 17.0, and 18.3 in the wet, moist, and dry scenarios, respectively), while field observations were longer, particularly in the dry scenario (Table 2). Smoke emissions for the simulated burns were predictably highest in the dry burns, with particulate matter (both PM_{10} and $PM_{2.5}$) much higher in the dry burns than either the moist or wet scenarios. No smoke emissions were measured in field burns, but since large fractions of smoke output are generated by smoldering (i.e., PM_{10}, $PM_{2.5}$, CH_4 and CO) these values would be expected to increase substantially in field burns where smoldering times were prolonged (e.g., dry burns; Table 2).

Simulations did not predict any mineral soil heating above lethal temperatures (>60° C; Table 2). Field burns surrounding individual pines, however, resulted in mineral soil heating across all moisture scenarios and to depths of 20-cm in mineral soil (Table 2). Dry burns resulted in elevated temperatures at 5- (mean duration = 61.3 min), 10- (mean duration = 9.7 min), and 20-cm below the surface (mean duration = 1.7 min).

Discussion

Since fire effects models predict only first-order fire effects, FOFEM and others and other fire effects models (Scott 1999, Fire Program Solutions 2003) generally underestimate mortality of large trees. In simulations of post-fire Sierra Nevada mixed conifer mortality, Stephens and Moghaddas (2005) estimated minimal mortality of large conifers (20.8% > 25cm DBH) from simulated fires, even though other studies in mixed conifer forests with similar fuel loading observed actual post-fire conifer mortality ranging between 64 and 100 % (Haase and Sackett 1998, Stephens and Finney 2002). Other investigators have found that post-smoldering mortality increases with tree diameter, or follow a U-shaped mortality probability distribution (McHugh and Kolb 2003). Patterns of mortality in this study changed with moisture scenario; there was minimal effect of diameter in wet and moist burns, whereas in dry burns mortality was highest in large diameter pines (Table 2). First-order fire effects on overstory trees are based on equations incorporating bark thickness and canopy height as the primary predictors of mortality. Given that significant soil heating has been linked to overstory stress and mortality in many forests (Swezy and Agee 1991, Haase and Sackett 1998), duff consumption and soil heating should be incorporated into these models to more accurately estimate post-fire mortality in long-unburned forests.

Soil heating in simulated fires grossly underestimated observed heating in actual fires. Long-duration mineral soil heating has been observed in many experiments at both the mescocosm and stand scale (Frandsen 1987, Frandsen 1991, Swezy and Agee 1991, Haase and Sackett 1998, Chapter 4), and anecdotal evidence from other forests is overwhelming. None of the simulations in this study resulted in lethal heating in mineral soil. Lethal heating (min > 60° C) was recorded here across all moisture regimes (Table 2); even the wet treatment heated surface soil (5cm) above the lethal threshold for three minutes. These observations of long-duration lethal heating suggest significant root and mycorrhizal damage (Flinn and Wein 1977), and a potential link resulting elevated mortality in restoration fires. Since duff fuels are the ultimate source of long duration soil heating, better models of duff ignition and consumption are needed (Frandsen and Ryan 1985, Hungerford et al. 1995, Frandsen 1997). This improved understanding of duff-soil heating will invigorate fire effects models and more accurately capture effects experienced by restorationists and fire managers in fire-excluded forests.

Duration of duff smoldering increased with decreasing duff moistures in both simulated and observed burns (Table 2), a result in line with previous duff smoldering research (Brown et al. 1991). The fact that simulations underestimated smoldering times is alarming, given the differences (duration of simulated smoldering in dry scenario = 18.3 min; observed = 179.8 min; Table 2) and the fact that wildfire-related mortality usually occurs under dry conditions. This non-linear increase in effects supports results of exaggerated levels of mortality in dry prescribed fires and in wildfires (Varner and Kush 2004, Varner et al. 2005).

Since duff consumption is a product of the duration of combustion, it is not surprising that these values followed the same patterns as duration of duff smoldering. Duff consumption was elevated in dry burns (Table 2), with each decrease in duff moisture corresponding to an approximate three-fold increase in fuel consumption in field burns. Simulations predicted no consumption (linked to the absence of smoldering) under wet and moist scenarios, and only minimal (8.1%) consumption in the dry scenario (Table 2). Given that duff consumption is a major objective of restoration burns in long-unburned southeastern pine forests (Hiers et al. 2003), this shortcoming is critical. A partial remedy is that empirical data from this study will be incorporated into the updated version of CONSUME. Simulation models still suffer from their reliance on empirical data. Future consumption models based on fundamental fuel characteristics (Sandberg et al. 2001) are an important step filling this understanding gap.

While smoke emissions were not measured in field burns, this comparison suggests some general conclusions. The production of smoke emissions is linked to their phase in combustion, and is therefore sensitive to durations of flaming and smoldering during fires (Sandberg et al. 2002). Smoldering phase combustion is responsible for dominant fractions of PM_{10}, $PM_{2.5}$, CH_4 and CO. In simulations under a dry scenario, 75.7 and 75.8 % of PM_{10} and $PM_{2.5}$ emissions were generated during the smoldering phase. Model corrections that account for longer smoldering times in observed burns would substantially increase these values. In the dry scenario the duration of smoldering was nearly 10 times that of the simulated burn (Table 2), a weighty implication given the human health hazards of particulate matter emissions (Sandberg et al. 2002) and increasing concern over greenhouse gases (Sandberg et al. 2002). Since duff smoldering is patchy and small-scale, these changes may be overstated. Future attempts at simulating emissions need to account for the heterogeneity in fuel consumption, duration of smoldering, and the emissions they generate.

Conclusions

The major finding of this study is the overwhelming need to validate models across the variation present in contemporary landscapes. Since most empirical data are gathered from operational burning, this inserts bias into the algorithms used in present models. Frequently burned stands will be frequently sampled, while degraded stands that burn infrequently (and formerly were rare in the landscape) will likewise be sampled infrequently. Even with imperfections, these models provide utility for large proportions of the landscape, and their weaknesses help identify gaps in both empirical and theoretical models. Incorporation of characteristics based on fuel properties (Sandberg et al. 2001) will improve these models in site-specific fires, as well as sharpen our understanding of the effects of fires on increasingly different ecosystems.

List of References

Agee, J. K. 2002. Fire as a coarse filter for snags and logs. Pages 359-368 in: W.L. Laudenslayer et al. (tech. coords). Managing dead wood in western forests. USDA Forest Service Gen. Tech. Rep. PSW-GTR-181. Pacific Southwest Research Station, Albany, CA.

Agee, J. K. 2003. Monitoring post-fire mortality in mixed-conifer forests of Crater Lake, Oregon. Natural Areas Journal 23:114-120.

Andrews, P. L. and C. D. Bevins. 2003. BehavePlus fire modeling system, version 3.0: User's Guide. USDA Forest Service Gen. Tech. Rep. RMRS-106. Rocky Mountain Research Station, Ogden, UT. 132 p.

Aresco, M. J. and C. Guyer. 1999. Burrow abandonment by gopher tortoises in slash pine plantations of the Conecuh National Forest. Journal of Wildlife Management 63:26-35.

Brose, P. and D.D. Wade. 2002. Potential fire behavior in pine flatwood forests following three different fuel reduction techniques. Forest Ecology and Management 163: 71-84.

Brown, J. K., E. D. Reinhardt, W.C. Fischer. 1991. Predicting duff and woody fuel consumption in northern Idaho prescribed fires. Forest Science 37: 1550-1566.

Covington, W.W., P.Z. Fulé, M.M. Moore, S.C. Hart, T.E. Kolb, J.N. Mast, S.S. Sackett, and M.R. Wagner. 1997. Restoration of ecosystem health in southwestern ponderosa pine forests. Journal of Forestry 95:23-29.

Engstrom, R. T., R. L. Crawford, and W. W. Baker. 1984. Breeding bird populations in relation to changing forest structure following fire exclusion: a 15-year study. The Wilson Bulletin 96: 437-50.

Eyre, F.H., ed. 1980. Forest cover types of the United States and Canada. Society of American Foresters, Washington, D.C. 148 pp.

Finney, M.A. 1998. FARSITE: Fire area simulator- Model development and evaluation. USDA Forest Service Research Paper RMRS- RP-4, Pacific Northwest Research Station. 17 p.

Fire Program Solutions. 2003. Users' Guide to Fuels Management Analysts Plus. Fire Program Solutions, LLC, Estacada, Oregon. 77 p.

Flinn, M.A. and R.W. Wein. 1977. Depth of underground plant organs and theoretical survival during fire. Canadian J. Botany. 55: 2550-2554.

Frandsen, W. H. 1987. The influence of moisture and mineral soil on the combustion limits of smoldering forest duff. Canadian Journal of Forest Research 17: 1540-1544.

Frandsen, W. H. 1991. Burning rate of smoldering peat. Northwest Science 65: 166-172.

Frandsen, W. H. 1997. Ignition probability of organic soils. Canadian Journal of Forest Research 27: 1471-1477.

Frandsen, W. H. and K. C. Ryan. 1985. Soil moisture reduces heat flux and soil temperatures under a burning fuel pile. Canadian Journal of Forest Research 16: 244-248.

Gilliam, F. S. and W. J. Platt. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. Plant Ecology 140:15-26.

Gordon, D.R. and J.M. Varner. 2002. Old growth longleaf pine restoration and management. Final Report to Eglin Air Force Base Jackson Guard, Niceville, Florida. 33 p. The Nature Conservancy, Altamonte Springs, Florida.

Haase, S.M. and S.S. Sackett. 1998. Effects of prescribed fire in giant sequoia-mixed conifer stands in Sequoia and Kings Canyon National Parks. Tall Timbers Fire Ecology Conference Proceedings 20: 236-243.

Hermann, S. H., ed. 1993. The longleaf pine ecosystem: ecology, restoration and management. Tall Timbers Fire Ecology Conference Proceedings 18. Tall Timbers Research Station, Tallahassee, Florida.

Heyward, F. 1939. The relation of fire to stand composition of longleaf pine forests. Ecology 20: 287-304.

Hiers, J. K., S. C. Laine, J. J. Bachant, J. H. Furman, W. W. Greene, and V. Compton 2003. Simple spatial modeling tool for prioritizing prescribed burning activities at the landscape scale. Conservation Biology 17:1571-1578.

Hungerford, R. D., W. H. Frandsen, and K. C. Ryan. 1995. Ignition and burning characteristics of organic soils. Tall Timbers Fire Ecology Conference Proceedings 19: 78-91. Tall Timbers Research Station, Tallahassee, FL.

Keane, R.E., K.C. Ryan, T.T. Veblen, C.D. Allen, J. Logan, and B. Hawkes. 2002. Cascading effects of fire exclusion in Rocky Mountain ecosystems: A literature review. Gen. Tech. Rep. RMRS-GTR-91. Fort Collins, CO: U.S. Department of Agriculture, Forest Service Rocky Mountain Research Station. 24p.

Kush, J. S. and R. S. Meldahl. 2000. Composition of a virgin longleaf pine stand in south Alabama. Castanea 65: 56-63.

Landers, J. L., D. H. Van Lear, and W. D. Boyer. 1995. The longleaf pine forests of the southeast: requiem or renaissance? Journal of Forestry **93**:39-44.

McHugh, C. W. and T. E. Kolb. 2003. Ponderosa pine mortality following fire in northern Arizona. International Journal of Wildland Fire **12:**1-16.

Mushinsky, H.R. 1985. Fire and the Florida sandhill herpetofaunal community: with special attention to the responses of *Cnemidophorus sexlineatus*. Herpetologica 4: 333-342.

Ottmar, R.D., M.F. Burns, J.N. Hall, and A.D. Hanson. 1993. CONSUME user's guide. Gen. Tech. Rep. PNW-GTR-304. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 17 p.

Ottmar, R.D. and R.E. Vihnanek. 2000. Stereo photo series for quantifying natural fuels. Volume VI: longleaf pine, pocosin, and marshgrass types in the Southeast United States. PMS 835. Boise, ID: National Wildfire Coordinating Group, National Interagency Fire Center. 56 p.

Ottmar, R.D., R.E. Vihnanek, and J. W. Mathey. 2003. Stereo photo series for quantifying natural fuels. Volume VIA: sand hill, sand pine scrub, and hardwoods with white pine types in the Southeast United States with supplemental sites for volume VI. PMS 838. Boise, ID: National Wildfire Coordinating Group, National Interagency Fire Center. 78 p.

Overing, J.D., H.H. Weeks, J.P. Wilson, J. Sullivan, and R.D. Ford. 1995. Soil survey of Okaloosa County, Florida. USDA Soil Conservation Service and Florida Agricultural Experiment Station, Gainesville, FL. 166 pp.

Provencher, L., A. R. Litt, and D. R. Gordon. 2003. Predictors of species richness in northwest Florida longleaf pine sandhills. Conservation Biology 17: 1660-1671.

Readle, E. L. 1990. Soil survey of Putnam County Area, Florida. USDA Soil Conservation Service and Florida Agricultural Experiment Station, Gainesville, FL. 224 pp.

Reinhardt, E. 2003. Using FOFEM 5.0 to estimate tree mortality, fuel consumption, smoke production, and soil heating from wildland fire. Sec. PS-2 in Proceedings of Fifth Fire and Forest Meteorology Conference, Orlando, FL.

Ryan, K. C. and W. H. Frandsen. 1991. Basal injury from smoldering fires in mature *Pinus ponderosa* Laws. International Journal of Wildland Fire 1:107-118.

Sandberg, D.V., R. D. Ottmar, and G.H. Cushon. 2001. Characterizing fuels in the 21st century. International Journal of Wildland Fire 10: 381-387.

Sandberg, D.V., R.D. Ottmar, J.L. Peterson, and J. Core. 2002. Wildland fire in ecosystems: Effects of fire on air. USDA Forest Service Gen. Tech. Rep. RMRS-GTR-42-vol. 5. Ogden, UT. 79 p.

Scott, Joe H. 1999. NEXUS: A system for assessing crown fire hazard. Fire Management Notes 59:20-24.

Stephens, S.L. 1998. Evaluation of the effects of silvicultural and fuels treatments on potential fire behaviour in Sierra Nevada mixed-conifer forests. Forest Ecology and Management 105: 21-35.

Stephens, S.L. 2004. Fuel loads, snag abundance, and snag recruitment in an unmanaged Jeffrey pine-mixed conifer forest in Northwestern Mexico. Forest Ecology and Management 199: 103-113.

Stephens, S.L. and M.A. Finney. 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. Forest Ecology and Management 162: 261-271.

Stephens, S.L. and J.J Moghaddas. 2005. Silvicultural and reserve impacts on potential fire behavior and forest conservation: 25 years of experience from Sierra Nevada mixed conifer forests. Biological Conservation 125: 369-379.

Swezy, D.M. and J.K. Agee. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Canadian Journal of Forest Research 21: 626-634.

van Wagtendonk, J.W. 1985. Fire suppression effects on fuels and succession in short-fire-interval wilderness ecosystems. Pages 119-126 in: Lotan, J.E., B.M. Kilgore, W.C. Fischer, and R.W. Mutch. Proceedings of a symposium and workshop on wilderness fire. Gen. Tech. Rep. INT-182. USDA Forest Service Int. Res. Station.

Varner, J. M., J. S. Kush, and R. S. Meldahl. 2000. Ecological restoration of an old-growth longleaf pine stand utilizing prescribed fire. Tall Timbers Fire Ecology Conference Proceedings 21: 216-219. Tall Timbers Research Station, Tallahassee, FL.

Varner, J.M. and J.S. Kush. 2004. Old-growth longleaf pine forests and savannas of the southeastern USA: Status and trends. Natural Areas Journal 24:141-149.

Varner, J.M., D.R. Gordon, F.E. Putz, and J.K. Hiers. 2005. Novel fire effects in southeastern pine forests: smoldering fire and overstory pine mortality. Restoration Ecology 13:1-9.

Wade, D.D. and J. D. Lunsford. 1989. A guide for prescribed fire in southern forests. USDA Forest Service Tech. Pub. R8-TP-11. Southern Region, Atlanta, GA. 56 p.

Figure 1. Location of study sites in northern Florida, USA. Both sites had undergone 37-40 y of fire exclusion prior to prescribed and simulated fires. Operational prescribed fires were conducted at Eglin Air Force Base. Small individual tree fires to evaluate mineral soil heating were conducted at the Swisher-Ordway Preserve.

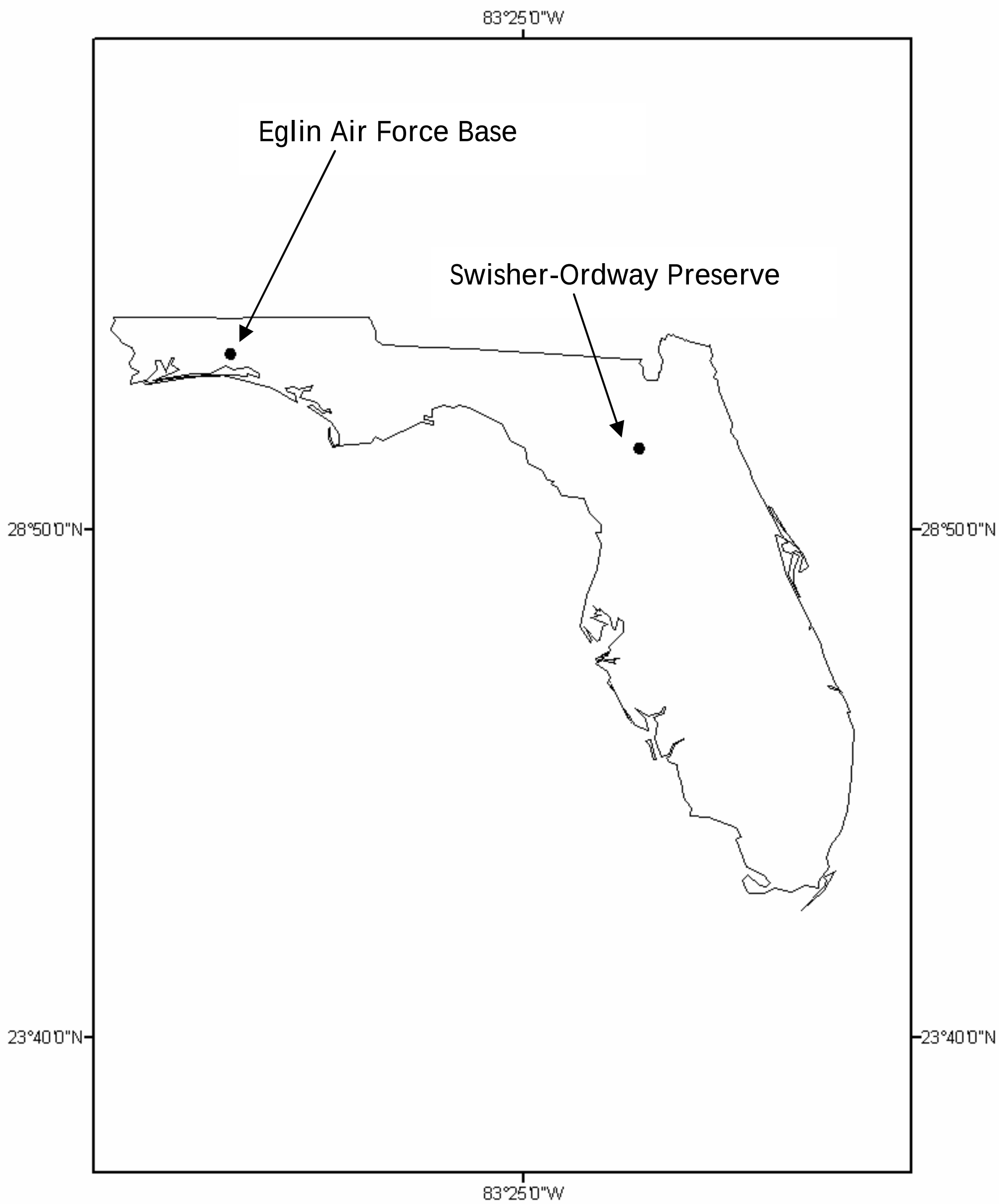


Table 1. Model inputs for simulations of fire effects (FOFEM 5.2.1) across three different moisture regimes in fire excluded longleaf pine stands in northern Florida, USA. Values were based on replicated operational prescribed burns at Eglin Air Force Base, Florida used in subsequent comparisons.

	Moisture Scenario		
Weather variables	Wet	Moist	Dry
Relative Humidity (%)	34	35	49
Air Temperature (°C)	14	19	26
Wind speed (at 6.1 m; m sec^{-1})	0.89	1.01	0.89
Fire behavior observations			
Flame length (m)	1.3	1.3	1.3
Fuel moisture variables[A]			
Oi (litter; %)	26	15	12
Oe (fermentation; %)	76	39	26
Oa (humus; %)	124	103	62
10-hour (%)	41	21	14
100-hour (%)	57	39	17
1000-hour (%) [B]	82	84	57
Fuel loading (kg ha^{-1})[A]			
1-hour	---------------	0.40	---------------
10-hour	---------------	0.66	---------------
100-hour	---------------	0.84	---------------
1000-hour	---------------	1.15	---------------
Litter	---------------	3.03	---------------
Duff	---------------	4.24	---------------
Live herbaceous	---------------	0.09	---------------
Shrub	---------------	0.35	---------------
Foliage	---------------	0.00	---------------
Branch	---------------	0.00	---------------
Total loading (kg ha^{-1})	---------------	10.76	---------------
Soil Inputs			
Soil texture	-------------	Coarse-Silt	------------
Soil moisture (A horizon; %)	12	8	4
FOFEM season of burn	--------------	Spring	---------------

[A] Fuel moisture data are from collected field data (R.Ottmar, unpublished data).
[B] 1000-hour fuel moisture contents are based on averages of collected sound and rotten downed fuels (R. Ottmar, unpublished data).
[C] Fuel loading data are a composite of collected field data (1-, 10-, 100-, and 1000-hr; litter and duff) and data from Ottmar and Vihnanek (2000) and Ottmar and others (2003).

Table 2. Comparison of results from simulated (FOFEM 5.2.1) and actual fires on fire-excluded longleaf pine forests at Eglin Air Force Base and the Swisher-Ordway Preserve in northern Florida, USA.

Parameter	*Simulated effects*			*Observed effects*		
	Wet	Moist	Dry	Wet	Moist	Dry
Soil heating						
Duration > 60°C (min) 5-cm	0	0	0	3.0	11.6	61.3
10-cm	0	0	0	0.8	9.2	9.7
20-cm	0	0	0	0.3	0.3	1.7
Fuel consumption						
Duff (% reduced)	0.0	0.0	8.1	5.0	14.5	46.5
Duration of smoldering (min)	6.8	17.0	18.3	9.4	40.4	179.8
Pine mortality probability (%)	35	35	35	0.5	3.0	20.5

10cm dbh class	69	69	69	0.0	0.0	6.7
20 cm dbh class	47	47	47	0.0	17.9	13.4
30 cm dbh class	30	30	30	3.2	3.3	30.0
40 cm dbh class	18	18	18	0.0	6.8	13.4
50 cm dbh class	12	12	12	3.2	3.3	30.0

Table 3. Modeled smoke output from simulated fires in fire excluded longleaf pine forests in northern Florida, USA.

	Simulated Emissions (kg ha^{-1}) Fuel moisture scenario		
Smoke Constituent	Wet	Moist	Dry
PM_{10}	58.0	69.6	95.5
$PM_{2.5}$	49.1	58.9	81.2
CH_4	25.0	30.3	43.7
CO	474.6	576.3	865.4
CO_2	13045	15168	16850
NO_X	20.5	23.2	24.1
SO_2	8.0	8.9	10.7

APPENDIX D.

J6E.2 THE INFLUENCE OF WEATHER ON COMBUSTION LIMITS IN A LONGLEAF PINE FOREST

Casey Anderson[A*], Sue Ferguson[A], Miriam Rorig[A], Kevin Hiers[B], Steve McKay[A], Mark Moore[A], Diana Olson[A], David Wright[A], Clint Wright[A], Bob Vihnanek[A], Roger Ottmar[A]

[A] USDA Forest Service, Pacific Northwest Research Station, Seattle Forestry Sciences Laboratory
[B] Jackson Guard, Eglin Air Force Base, FL

1.0 INTRODUCTION

While the benefits of prescribed fire are generally understood, the environmental conditions needed to accurately achieve desired consumption values are not well quantified. The influence of weather on the moisture of woody fuel has been studied extensively, yet much of the research has focused on the conditions required for wildfire initiation and is less appropriate for the combustion processes in prescribed fire.

In order to better quantify the effects of weather on moisture dynamics and associated consumption values in a longleaf pine (*Pinus palustris* Mill.) forest, a series of experiments were set up in both 2001 and 2002. During both years, controlled burns were conducted under a variety of moisture conditions and an array of portable weather stations monitored both meteorological conditions and forest floor moisture levels.

2.0 SITE DESCRIPTION

The two study areas used were located on Eglin Air Force Base in the Florida Panhandle. Prescribed burns were conducted at the Ramer Tower study area in 2001, and at both the Ramer Tower study area and the Ranger Camp study area in 2002. These sites lie approximately 20 miles apart and contain sets of individual units roughly 25 ha each. In addition to longleaf pine, the overstory vegetation consisted of turkey oak (*Quercus laevis*), sand live oak (*Quercus geminata*), and sand pine (*Pinus clausa*). Yaupon (*Ilex vomitoria*) and Palmetto (*Serenoa repens*) were common understory shrubs. The terrain in the area is relatively flat and 200 feet above sea level.

At the Ramer Tower study area, 4 units were burned in 2001 and three units were burned in 2002. The Ranger Camp study area contained two adjacent blocks of units, labeled mesic and xeric, each containing three units which burned in 2002. The mesic and xeric units were labeled based upon slight differences in the vegetation structure and an elevation difference of a few meters.

* *Corresponding author address:* Casey Anderson, USDA Forest Service, PNW Research Station, Seattle Forestry Sciences Lab, 400 N 34th St Ste 201, Seattle, WA 98103; email: canderson@fs.fed.us

2.1 *Data Collection*

Six weather stations were set up in 2001 for varying lengths of time to monitor conditions at the Ramer Tower site. One of these stations, Eglin 1, was left in place to monitor the 2002 burns and as of August 2003 is still collecting data. Two weather stations (Eglin 12 and 13) were set up at Ranger Camp in January of 2002 and collected data until May 2003. For the purposes of this paper, only the data from Eglin 1, 12, and 13 will be presented as these three stations provide the longest and most complete data record available.

All weather stations measured air temperature, relative humidity, wind speed, and wind direction. Additionally, stations 1, 12 and 13 measured 10 hour fuel temperature, 10 hour fuel moisture, barometric pressure, and precipitation. Sensors at all stations had a sampling interval of 10 seconds and logged data averages every 15 minutes.

Forest floor moisture was monitored at all stations using Campbell Scientific model CS-615 time-domain reflectometer (TDR) probes. These TDRs consisted of two parallel wave guides 3.2 mm in diameter, 30 cm long, and 3.2 cm apart. The period of the electromagnetic signal traveling down the wave guides is influenced by the moisture level of the surrounding material. Therefore, varying moisture conditions are represented by changes in the signal's period. The CS-615 probes have an operational period range from 0.7 to 1.6 ms. All weather stations sampled and logged the raw period output from the CS-615 probes. We refer to this uncalibrated output as the moisture index (MI).

Two to four moisture probes were inserted either horizontally or vertically into the forest floor organic layer at each station, at varying depths. Litter (needles and bark slough with no evidence of decay) and duff (decomposing organic material) layers were highly variable across the landscape, with shallow layers (1-5 cm litter, 1-5 cm duff) in open areas and significantly thicker layers (5-10 cm litter, 5-10 cm duff) surrounding the base of most large longleaf pine trees. In all locations, the underlying mineral soil was well drained sand.

2.2 *Burn Thresholds*

For each prescribed fire, pre- and post-burn fuel loadings were measured at a set of 30 plots per unit set in a 1 chain (66-foot) grid. The fuel loadings in the

Unit Name	Date of Burn	Time of Ignition	Duff MI	Plot Pin Duff Consumption (percentage by depth)	Tree Pin Duff Consumption (percentage by depth)
Ramer Tower Inner North	2/18/2001	1200	*	2	3
Ramer Tower Outer South	3/27/2001	1000	0.863	2	7
Ramer Tower Inner South	4/26/2001	1000	0.800**	9	50
Ramer Tower Outer North	9/21/2001	1200	0.772	27	66
Ramer Tower East	2/22/2002	1030	0.848	2	15
Ramer Tower West	3/5/2002	930	0.857	5	4
Ramer Tower Mid	3/24/2002	1100	0.824	13	30
Ranger Camp Xeric NW	3/8/2002	1100	0.894	18	26
Ranger Camp Xeric NE	3/14/2002	1300	0.922	3	6
Ranger Camp Xeric Mid	4/7/2002	1700	0.867	24	52
Ranger Camp Mesic Mid	2/22/2002	1400	0.882	9	24
Ranger Camp Mesic SE	3/4/2002	1400	0.906	2	17
Ranger Camp Mesic SW	4/24/2002	1320	0.828	25	57

Table 1. List of the 2001 and 2002 prescribed fires used in this study.
* Weather station not installed for this burn.
** Estimated value, weather station offline from 0800 to 1130 on day of burn

forest floor organic layer are the only ones used in this study. By conducting prescribed burns on adjacent units under differing moisture conditions, a range in forest floor consumption was achieved. The consumption values in table 1 show good correspondence between duff consumption amount and relative TDR duff moisture level at the time of ignition. Using this relationship, burn thresholds were defined at the upper and lower limits of the TDR-measured moisture indexes. These thresholds correspond to the wettest (least overall consumption) and driest (most overall consumption) fires at the Ramer Tower site in 2001 and at the Ranger Camp site in 2002. These thresholds do not however represent the full range within which prescribed burning occurs. Figure 1 shows the wet and dry thresholds superimposed upon a time series of moisture index for the duff layer from Eglin 1. The wet and dry thresholds correspond to the moisture indexes at the time of ignition for the burns on days 86 and 264, respectively. Observed data are posted to the website www.fs.fed.us/PNW/AIRFIRE/fm each day so that burn managers in the area can track the moisture index as it relates to these thresholds and anticipate whether maximum or minimum consumption may occur based upon observed moisture levels.

3.0 DEVELOPMENT OF A LITTER MODEL

As is described in Ferguson et al. (2002), a study of the relationship between the Eglin 1 litter layer moisture index and wind, relative humidity, temperature and precipitation found that nearly all of the variability in the moisture index could be explained by the previous day's MI and precipitation. A multiple linear regression of the moisture index for probe 1A at time t ($MI1A_t$) with the previous day's moisture index ($MI1A_{t-1}$), the square root of the past 24 hour precipitation (P_t) and the square root of the precipitation from the previous 24 hour period (P_{t-1}) yields the equation:

$$MI1A_t = 0.9957 \times MI1A_{t-1} + 0.0023 \times \sqrt{P_t} - 0.0013 \times \sqrt{P_{t-1}} \quad (1)$$

This regression has a multiple r^2 value of 0.9997 and a correlation value of 0.9533. Moisture index values and 24 hour precipitation totals (in 0.01 mm) at 1300 LST from days 55 through 219 2001 were used to derive the regression. When tested on days 220 through 335 2001, the correlation value was 0.9212.

This type of equation could be very helpful in trying to determine future moisture levels in the forest floor organic layer. When coupled with defined burn thresholds, a prediction can be made of the number of days following a rain event needed to sufficiently dry the forest floor below the wettest burn threshold. An estimate can also be made for the amount of rain needed to lift the forest floor moisture above the dry threshold to avoid a prescribed fire of high intensity.

4.0 DEVELOPMENT OF A DUFF MODEL

Given the high correlation values for the litter layer prediction in Ferguson et al. 2002, the same approach was used to fit a model to the duff layer at the same location for the same time period. Again, 1300 LST values were used to filter out the diurnal cycle and to create a model consistent with the National Fire Danger Rating System, which uses 1300 LST observations to calculate its indexes. Many predictors, including past 24-hour average relative humidity, past 24-hour average 10 hour fuel moisture, past 24-hour precipitation duration, and past 48-hour precipitation were tested in multiple linear regressions. Once again it was found that the three predictors used in the litter equation yielded the highest r^2 and correlation values for a prediction of the duff layer moisture. Some predictors, such as past 24-hour precipitation duration, also fit quite well, but

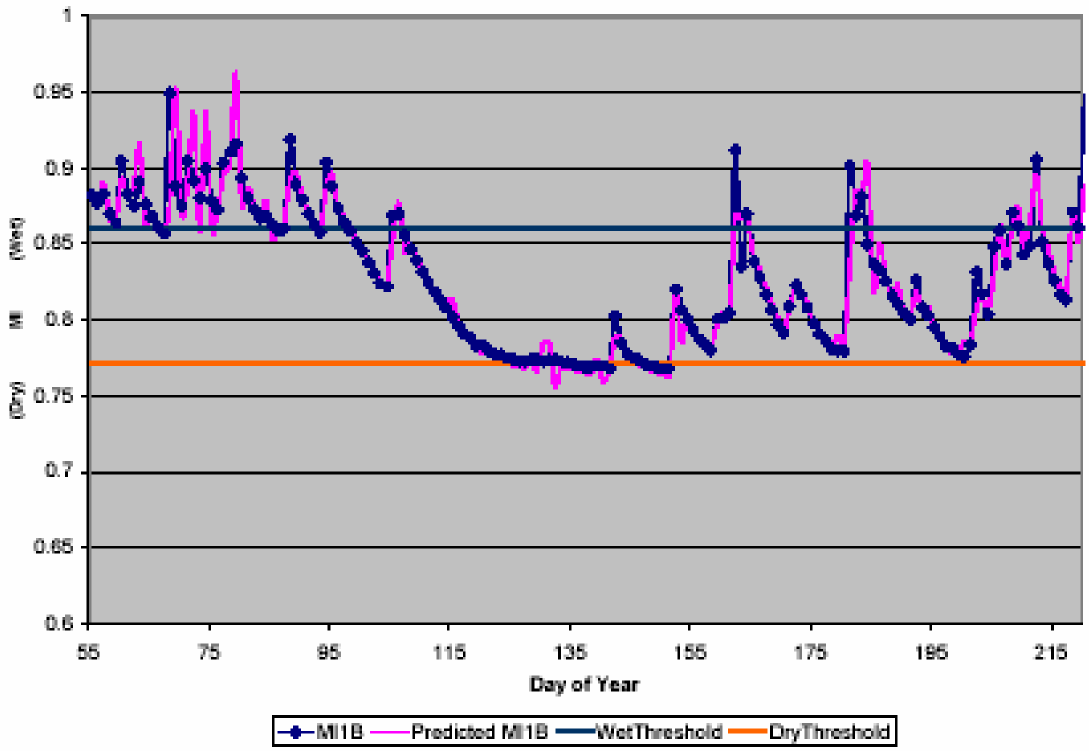


Fig. 1. A time series of moisture index for probe 1B (MI1B), the predicted MI for probe 1B and the wet and dry thresholds.

the correlation values were not as high as for the total past 24-hour precipitation amount.

A multiple linear regression of the moisture index 1B with the previous day's moisture index ($MI1B_{t-1}$), the square root of the past 24 hour precipitation (P_t) and the square root of the precipitation from the previous 24 hour period (P_{t-1}) gives the equation:

$$MI1B_t = 0.9938 \times MI1B_{t-1} + 0.0029 \times \sqrt{P_t} - 0.0016 \times \sqrt{P_{t-1}} \quad (2)$$

with an r^2 value of 0.9997 and a correlation value of 0.95.

Figure 1 shows a time series of the 1300 LST moisture index 1B prediction as well as the actual values for the development period in 2001. The plot shows that the prediction works well during dry periods but has some trouble accurately capturing wetting periods. Overall, the mean absolute error for the model is 0.0080. Separating the days with rain from the days without rain gives an idea of the differing model performance for the two phases. Mean absolute error is 0.0037 for days without rain and 0.0135 for days with rain.

Visual inspection of the time series of the moisture index and precipitation indicates that for any given amount of rain, the moisture index response is not consistent. We hypothesize that a short intense rainfall is less effective at wetting the forest floor than a longer, less intense rain event of the same magnitude. Additionally, it appears that the forest floor organic layers are somewhat hydrophobic when the moisture index drops to very low levels. When the forest floor is very dry, it appears to require an as-of-yet unquantified volume of rain for the moisture index to noticeably respond.

These differing trends in forest floor wetting are likely to be the cause of the poorer model performance on days with rain as opposed to rainless days.

To further test the application of this type of predictive model, multiple linear regressions were performed using data from weather stations Eglin 12 and Eglin 13. These regressions are based upon data from 2002 and 2003. Again predictive equations were developed that were consistent in accuracy with the Eglin 1 predictions. Some of the same patterns were also found. The same predictive variables yielded the highest correlation, and drying was better predicted then wetting.

5.0 A DRYING CALCULATOR

To best utilize the predictive equation developed for the duff layer at Eglin 1 in an easy to use format, a

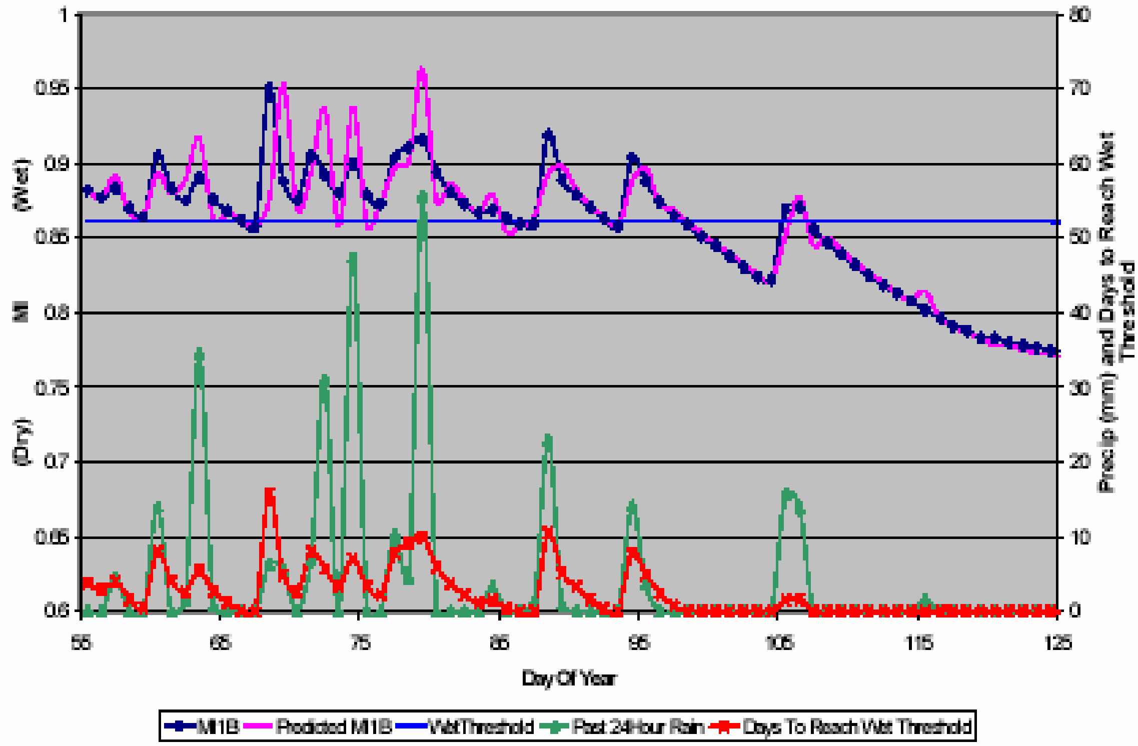


Fig. 2. A time series of moisture index for probe 1B (MI_{1B}), predicted moisture index, rain, and the number of dry days need for the MI to reach wet threshold.

website will be created that employs a calculator to predict future moisture index values. Using the current moisture index and past precipitation totals, equation 2 is used to calculate the number of dry days needed to reach either the wet or the dry burn threshold. This provides a quick forecast that can be used to anticipate the timing for fuel conditions to reach a desirable level for prescribed fire operations.

The accuracy of the moisture index prediction degrades with time. Mean absolute error increases from 0.0082 to 0.0188 as the prediction extends from 1 to 7 days out. The accuracy of the drying calculator's prediction can be examined in Figure 2. Notice the rain event on day 88 of 2001 and the dry period that followed. On day 88, the past 24 hour rain amount totaled 23 mm and the 1pm MI of probe 1B (MI_{1B}) had peaked at 0.919. Given this MI value, the drying calculator predicts that 10 dry days are required for the MI_{1B} to drop below the wet burn threshold. The MI_{1B} actually dropped below the threshold in 4 days, significantly faster than the predicted 10 days. However, on day 89, after 24 hours of drying, the drying calculator predicts 5 dry days are needed to drop the MI_{1B} below the wet burn threshold. This is much closer to the 3 days actually needed for the drying to occur. The same pattern is found for the rain events on day 63 and 94. The predicted number of drying days are much more accurate after one day of drying has already occurred. Therefore, it appears that the drying calculator performs significantly better 24 hours after a rain event then directly after a rain event.

6.0 CONCLUSIONS

A simple model developed from a multiple linear regression of past moisture index and past precipitation can provide a useful tool for predicting the evolution of future moisture conditions. By using a long time series of continuous data in 2001 to derive the equation, correlation values remain high when tested against data in 2002 and 2003.

7.0 REFERENCE

Ferguson SA, Ruthford JE, McKay SJ, Wright D, Wright C, Ottmar R (2002) Measuring moisture dynamics to predict fire severity in longleaf pine forests. *International Journal of Wildland Fire*, **11**, 1-14.

APPENDIX E.

Tree mortality resulting from re-introducing fire to long-unburned longleaf pine forests: The role of duff moisture in fire damage

J. Morgan Varner, III,[1, 2] **Francis E. Putz, Doria R. Gordon,** School of Natural Resources and Environment, University of Florida, Box 118526, Gainesville, FL 32611-8526, U.S.A.
J. Kevin Hiers, [3] Eglin Air Force Base, Jackson Guard, Niceville, FL 32570, U.S.A.
Roger D. Ottmar, Fire and Environmental Research Applications Team, Pacific Wildland Fire Sciences Laboratory, USDA Forest Service Pacific Northwest Research Station, Seattle, WA 98103, U.S.A.
Robert J. Mitchell, J.W. Jones Ecological Research Center, Newton, GA 31770, U.S.A.
Dale D. Wade, USDA Forest Service, Southern Research Station, Athens, GA 30602

[1]**Corresponding author (e-mail: jmvarner@humboldt.edu)**
J. Morgan Varner, III
Department of Forestry and Watershed Management
Humboldt State University
1 Harpst Street
Arcata, CA 95521, U.S.A.
(707) 826-5622 Tel.
(707) 826-5634 Fax.

[2] Present address: Department of Forestry and Watershed Management, Humboldt State University, 1 Harpst Street, Arcata, CA 95521
[3] Present address: The Nature Conservancy of Georgia, Thomasville, GA 31792, U.S.A.

Abstract: Restoring fire to long-unburned forests, woodlands, and savannas often causes widespread mortality of large trees. To better understand this phenomenon, we subjected 16 fire-excluded (35-45 y since fire) longleaf pine stands in northern Florida, USA to one of four burning treatments based in the moisture content (% of dry weight) of the Oe and Oa horizons (hereafter referred to as "duff"): wet (moisture content 120% of dry weight); moist (90% moisture content); dry (60% moisture content); and, a no-burn control. Two and three years after experimental fires, overstory pines in the dry treatments suffered the greatest mortality (mean = 20.5%), whereas the wet and moist treatments did not differ from the control treatment in pine mortality (0.5 % and 1.0 % vs. 3.0 %, respectively). Across the treatments, fire-induced reductions in duff depth were greatest in the dry treatment, averaging 3.8 cm (46.5%) consumed compared with the moist (1.4 cm, 14.5%) and wet (0.6 cm, 5%) treatments. In a logistic regression model with individual trees nested within our three burning treatments the best predictors of individual pine mortality were duff consumption and percent of canopy scorched ($P< 0.001$; $R^2= 0.34$). In this model, canopy scorch was only significant in the dry burning treatment, while duff consumption was significant across all treatments. Duff consumption was related to pre-burn lower duff (Oa) fuel moisture content ($R^2 = 0.78$, $P <0.001$). Restoration and management of fire-excluded longleaf pine forests will require development of burn prescriptions that include both the effects of flaming combustion and residual smoldering fires, critical fire effects in these fire-excluded coniferous forests.

Key Words: ecological restoration, *Pinus palustris*, prescribed fire, smoldering duff fires, tree mortality

Introduction

Active fire suppression, landscape fragmentation, and exurbanization have altered the frequency, intensity, and severity of fire in many contemporary landscapes (Agee 1993, Minnich et al. 1995, Ottmar et al. 1998, Outcalt 2000, Busse et al. 2000, Barton 2002, Wright and Agee 2004). In ecosystems maintained by frequent low-intensity fires, reduction in fire frequency leads to increased tree and shrub density, changed species composition, altered nutrient cycles, and fuel accumulation (Heyward 1939, Cooper 1960, van Wagtendonk 1985, Ware et al. 1993, Covington and Moore 1994, Minnich et al. 1995, Gilliam and Platt 1999, Everett et al. 2000, Varner et al. 2000, Keane et al. 2002, Wright and Agee 2004). When fires do occur after a prolonged period of suppression, these changes in the fuel environment result in altered fire behavior and effects (Johnson and Miyanishi 1995). Although reinitiation of historic fire regimes is a major component of most approaches to restoring fire-suppressed forests, woodlands, and savannas worldwide, burning often fails to achieve the desired results (Fulé et al. 2004, Varner et al. 2005).

Among the greatest challenges to restoration of fire regimes after long periods of fire suppression is excessive tree mortality when fires are re-introduced (Wade et al. 1997, Varner et al. 2000, Stephens and Finney 2002, McHugh and Kolb 2003, Fulé et al. 2004, Varner et al. 2005). Overstory mortality in "restoration fires" can be as high as 75 – 95%, causing radical shifts in ecosystem structure and composition (Varner et al. 2000, Gordon and Varner 2002). In ecosystems maintained by frequent low-intensity fires, the likelihood of fire-induced mortality generally decreases with increasing tree diameter (e.g., Ryan and Reinhardt 1988, Peterson and Ryan 1985, Wade and Johansen 1986, Ryan et al. 1988). By contrast, in restoration fires, tree mortality follows varying patterns, sometimes increasing with increasing tree diameter (Varner et al. 2000, Kush et al. 2004) and occasionally with bimodal peaks of mortality in small and large diameter trees (Swezy and Agee 1991, McHugh and Kolb 2003). The mechanism responsible for mortality caused by restoration fires is unclear, with different investigators emphasizing damage to canopy (Wyant et al. 1986, Ryan and Rheinhardt 1988, Menges and Deyrup 2001), stem vascular tissue (Ryan and Frandsen 1991, McHugh and Kolb 2003), and root tissues (Swezy and Agee 1991, McHugh and Kolb 2003), as well as indirect effects of these damages on tree stress and defense against pathogens (Ostrosina et al. 1997, Ostrosina et al. 1999, Menges and Deyrup 2001, Feeney et al. 1998, Wallin et al. 2003, McHugh et al. 2003). Determining causes of fire damage could help managers predict fire-caused mortality and inform burn prescriptions to avoid or reduce post-fire tree mortality.

Restoration of longleaf pine (*Pinus palustris* Mill.) ecosystems in the southeastern USA after long periods of fire suppression is a major conservation and management goal (Hermann 1993, Landers et al. 1995, Wade et al. 1997, Johnson and Gjerstad 1998, Varner et al. 2000). Reference longleaf pinelands have park-like stand structure, are mono-dominant, and have a fire return interval of 1-5 years (Christensen 1981, Robbins and Myers 1992). Since European settlement, 97% of longleaf pinelands have been lost (Frost 1993) and only half of all remnant pinelands are burned regularly (Outcalt 2000). Where fire has been reintroduced, overstory pine mortality rates have often been high, at times reaching 75-95% of large trees, and community shifts have been outside the range of historic variability (Varner et al. 2000, Kush et al. 2004), thus defeating restoration goals. This disconnection between restoration objectives and outcomes has confounded pineland restoration efforts region-wide (Varner et al. 2005).

In 2001, we initiated a large-scale restoration experiment to examine the causes of mortality in long-unburned (ca. 35-45 years since fire) longleaf pine forests. We examined the effects of damage to canopy, stem, and roots at the stand and individual tree levels. Motivated by the reported correlations of conifer decline and mortality with duff consumption (Busse et al. 2000, Stephens and Finney 2002, Elliott et al. 2002, McHugh and Kolb 2003), we used varying duff (Oe and Oa soil horizons) volumetric moisture contents to determine the role of smoldering duff in pine mortality (Ferguson et al. 2002). We tested the effects of tree, fuel, and burn characteristics as predictors of overstory pine mortality in restoration fires. We hypothesized that larger trees have greater duff accumulation and that duff moisture is correlated with duff consumption during fires and subsequent post-fire mortality. Finally, we review weather parameters associated with duff moisture patterns to develop criteria for safely reintroducing fire to stands with duff accumulation.

Materials and methods

Study area

We conducted experimental burns in four long-unburned (from ca. 35 to 45 years since fire) longleaf pine forests at Eglin Air Force Base on the Florida Panhandle, USA (N 30° 38', W 86° 24'; Figure 1). All stands had heavy downed woody and duff fuel loading (ranging from 14 to 34 tons ha^{-1}), remnant longleaf pine overstory (45-200 trees > 10 cm DBH ha^{-1}), and altered midstory and canopy tree species composition typical of long-unburned pine forests of the southeastern Coastal Plain (Gilliam and Platt 1999, Kush and Meldahl 2000). All sites are within the Southern Pine Hills District of the Coastal Plain Physiographic Province with deep, well-drained sandy soils (Brown et al. 1990). Soils of the study sites were all typic quartzipsamments of the Lakeland series with mean depth to water table exceeding 200 cm (Overing 1995). The climate of the area is subtropical, characterized by warm, humid summers and mild winters, with mean temperatures of 25° C and mean annual precipitation of 1580 mm, most of which falls from June to September (Overing 1995). Elevations of the study sites are 52-85 m asl and all sites have typical sandhill topography with minimal effects of slope and aspect (Myers 1990).

Four 10 ha stands at each of four sites were randomly assigned to one of four burning treatments based on day-of-burn volumetric duff moisture content (vdmc; percent of dry weight): dry (60% vdmc); moist (90% vdmc); wet (120% vdmc); and a no-burn control. For each experimental fire, we recorded fire weather, fuel moisture, and fire behavior (Table 1). Within each replicate plot, we randomly selected 50 pines for fire effects sampling. All prescribed burns were ignited during the late dormant season (February to April). To minimize variation in fire behavior, all fires were ignited using strip head fires or spot-grid ignition (Wade and Lunsford 1989), with ignition managed to minimize variation in flame lengths and rate of spread.

Data Collection

Characteristics of ground fuels and vegetation were measured in each plot prior to burning. We measured forest floor depth by horizon (litter [Oi horizon] and duff [Oe and Oa horizons]) at the base of each of the > 20 cm dbh plot trees. In each plot we estimated total woody fuel loading using Brown's (1974) planar intercept method. Forest floor depth was measured at each tree using eight 20 cm pins buried flush with the litter surface and offset from the stem approximately 10 cm at cardinal and ordinal directions. Within 5 cm of each pin, the composition (material and depth of Oi, Oe, and Oa forest floor horizons) was described with little disturbance to the fuelbed. For all overstory pines (> 15 cm dbh; dbh =stem diameter at 1.37 m), we recorded their dbh, total height, crown height, and distance and direction to plot centers.

Initial post-burn measurements were made on all trees 3 to 4 weeks following the experimental fires. Stem char height (in cardinal directions at each tree) was measured on all trees with a height pole at four cardinal directions. Scorch height, maximum height of needle consumption, and percent of canopy volume scorched were estimated on all plot trees using a clinometer. Post-fire reductions in forest floor depth at individual trees were measured as the average difference between the pre- and post-fire exposure of duff pins. Basal damage and evidence of pathogens were noted for all plot trees. Following initial post-burn surveys, we surveyed tree mortality and any signs of decline or disease 6, 12, 18, and 24 months post-burn to capture the temporal patterns of mortality.

For all 2002 burns, rates of radial stem growth were determined for 15 trees two years following burns. From each randomly selected tree per plot, we extracted two 5 cm cores at 1 m height using an increment borer. Two cores per tree were extracted to better detect locally absent rings. All cores were dried, mounted, and sanded according to standard dendrochronological techniques prior to measurement (Stokes and Smiley 1968, Fritts 1976). Ring width was measured to the nearest 0.01 mm using a binocular microscope. Ring width was determined for the two years prior to burns (2000-2001) and the two years following burns (2002-2003). To compare treatments, we calculated plot means of the percent change in annual radial increment per tree.

Data analysis

The study was designed as a randomized block design with four treatments and four replicates per treatment. The four treatments were based on day-of-burn volumetric duff moisture content. Within each treatment plot, 50 trees were nested to model predictors of individual tree mortality.

At the burn block level, we used analysis of variance to detect effects of treatment duff moisture (wet, moist, dry, control) on pine mortality. If differences were detected, we used a post-hoc Tukey's HSD to detect differences among treatments. We used the same design to test for effects of duff moisture treatments (wet, moist, dry) on forest floor reduction (cm and %), stem char height, canopy damage (scorch %, scorch height, and % canopy consumption), and changes in radial growth. When necessary, non-normal data were transformed to meet the assumptions of parametric analyses. Fuel environment parameters tested were: ambient relative humidity (%); ambient air temperature; moisture contents of litter (Oi), fermentation (Oe), and humus horizons (Oa); and, moisture contents of 10-, 100-, and 1000-hour fuels. We also tested the role of crown scorch (plot means of scorch height and percent of canopy volume scorched), height of stem char, and duff consumption on pine mortality.

Given the within-plot variation in fire effects and post-fire tree mortality, we modeled individual tree post-fire mortality using nested logistic regressions (Stephens and Finney 2002). We modeled probability of pine mortality as a function of pre-burn fuel characteristics (dbh, pre-fire duff depth, crown height, total tree height), duff moisture treatment, and fire effects (% duff consumed, duff depth reduction, char height, % crown scorch, and scorch height). To rank competing regression models, we used Akaike's Information Criteria (AIC), where lower values represent the best approximating model.

Results

Duff consumption, stem char, and canopy damage varied among the 12 experimental fires (Table 2). Across all twelve burns, mean duff consumption at the bases of the pines ranged from 2 to 63% (0.2-6.2 cm). Duff consumption in the dry burns was nearly an order of magnitude greater than in wet burns and three times greater than in moist burns (Table 2). Mean height of stem char was 2.24 m across all burns; individual plot means ranged from 0.9 to 5.1 m with no apparent treatment effect (Table 2). Mean percent of pine canopy scorched and scorch height ranged from 4.3 to 71.7 % and 3.5 to 16.7 m, respectively, across all burned plots and also did not vary among treatments (Table 2). Due to the low intensity of all the prescribed burns, only 3 trees (< 0.7% of all burned trees) suffered any needle loss during the fires; needle consumption did not exceed 10% of the total canopy volume of any tree and was therefore not included in the analyses.

Overstory longleaf pine mortality for all plots during the first two years after the fires ranged from 0 to 42 percent, with only three plots exceeding 10 percent mortality (Table 2). Soon after the fires, all pines in the burned plots produced new foliage and none showed obvious signs of decline; mortality generally lagged 12 to 18 months after fires. All the trees that died showed signs of bark beetle (primarily *Dendroctonus terebrans* and, *Platypus spp*.) attack, as did several surviving pines. Overstory pine mortality during the first two years after the fire differed among treatments; dry burns averaged 20.5% mortality, moist burns averaged 3.0 %, and wet and control burns suffered < 1% mortality (Figure 3; $F= 10.56$, $df = 12$, $p < 0.001$). Variation in mortality rates was greatest among the dry burns, where overstory pine mortality ranged from 8-42%.

Univariate linear regressions revealed that pine mortality was related to various parameters describing the fuel environment and fire effects. Among fuel environment variables, ambient air temperature, 100-hour fuel moisture, and both Oe and Oa horizon fuel moisture were all significantly ($p < 0.05$) related to mortality (Table 3). The best fuel environment predictors were Oa and 100-hour fuel moisture, explaining 50 and 47% of variation in pine mortality in univariate linear regressions, respectively. Among fire effects variables, consumption of forest floor (litter plus duff), duff consumption, and stem char were significantly ($p< 0.05$) related to overstory pine mortality (Table 3). Forest floor reduction alone explained 71% of the variation in overstory pine mortality. At the whole plot level, when all fuel environment and fire effects variables were included in a multiple regression, the model with the highest R^2 (0.57) and lowest AIC (5.1) included only % duff reduction ($p<0.01$):

log pine mortality (%) = -2.93 + 0.15 (% duff reduction).

As tree dbh increased, so did fire-induced mortality ($p=0.01$), but only 2% of the variation in mortality was explained by dbh (Figure 4; Table 5,). Across all treatments over the two years after the fires, two classes of small diameter trees (15-25 and 25-35 cm; n=116 and 176 trees respectively) both experienced 20% mortality over the study period; larger trees (35-45, 45-55 and >55 cm; n=126, 25, and 5 trees, respectively) suffered 36, 50, and 80% mortality, respectively. Live crown ratio was significantly related to overstory mortality ($p = 0.02$), but explained little variation in mortality (Table 5).

Across treatments, patterns in pine radial growth mimicked patterns in overstory pine mortality. Ring widths for post-burn years 2002 and 2003 were higher for control and wet burns, with moist and dry having the lowest earlywood values.

The results of the logistic regression of individual tree mortality supported the importance of fire effects parameters demonstrated in the plot-based analyses. Combining trees from all of the treatments in a nested logistic regression model (Stephens and Finney 2002) revealed that the likelihood of a tree dying was related to a combination of canopy scorch and duff consumption (Table 5; $R^2 = 0.31$, $P < 0.001$). No fuel environment parameters were incorporated into this model because fuel environment variables were measured at the plot level, not at individual plot trees, which possibly explains the low R^2 value observed. Our model of mortality as related to scorch and duff consumption nested within treatment explained 34% of the variation in mortality (Table 6; $p < 0.0001$). This analysis revealed that while duff consumption was an important factor across all treatments, canopy scorch was significant only in the dry burning treatment.

Discussion

Restoration of long-unburned southeastern pine forests is complicated by the often opposing goals of reducing fuels and retaining mature overstory pines. In this study, maximum fuel reduction was linked strongly to the greatest loss of overstory pines. Further, although most models of fire-caused mortality assume that as tree size, bark thickness, and canopy height increase, so does resistance to fire damage (e.g., Martin 1963, Ryan et al. 1988, Dickinson and Johnson 2001), our restoration fire-caused longleaf pine mortality rates increased with increasing tree size (Figure 4). This pattern appears related to the deeper accumulations of forest floor fuels around the bases of large trees ($P<0.001$; $R^2 = 0.18$). Given that other investigators have also observed post-fire reductions in survival (Varner et al. 2000, Stephens and Finney 2002, McHugh and Kolb 2003) and growth (Busse et al. 2000, Elliott et al. 2002) with fire-caused reductions in forest floor and duff, these results may be relevant to other conifers.

Fire-induced overstory pine mortality lagged 12 to 18 months after the burns. A similar pattern has been observed by other researchers (e.g., Wyant et al. 1986, Stephens and Finney 2002) and noted anecdotally by longleaf pine resource managers (Varner et al. 2005). This lag may have been due to the fact that the large, old trees had several predisposing mortality factors (i.e., reduced physiological condition, high root volumes in drought-prone duff, high stand density resulting from fire exclusion) in addition to the fire injuries to roots, cambia, and canopy meristems. Kelsey and Joseph (2003) suggest that the fire-caused root damage may lead to chronic water stress and subsequent declines in tree defenses. Delayed mortality may have also been caused by reduced allocations to defense leading to attack by beetles or susceptibility to fungal pathogens, both common consequences of restoration fires (Ostrosina et al. 1997, Ostrosina et al. 1999, Menges and Deyrup 2001, Kelsey and Joseph 2003). Future work is needed on the physiological mechanisms of decline and mortality in response to fire damages (see below).

Mortality and Fire Damage to Stem, Canopy, and Roots

Stem char has been correlated with decreased growth and increased tree mortality in studies of other conifers (e.g., van Wagner 1973, Dixon et al 1984, Peterson and Arbaugh 1986, Wade and Johansen 1986) and increasing char heights were positively related to longleaf pine mortality in our study (Tables 3, 5). This variable may have been dropped from the whole model tests of multiple variables because of the high correlations between char height and crown scorch volume ($r=0.70$) and scorch height ($r= 0.78$). Our exclusion of small (dbh < 15 cm) fire-susceptible trees may also have reduced the overall effect of char height on tree mortality in our study. It seems important to note, however, that measurements of char do not capture the results of long-duration heating during the smoldering phase of combustion. McHugh and Kolb (2003) supplemented char height measurements with char severity (= bark damage) and found strong links with post-fire mortality. Given the high correlation between char height, canopy damage, and fire behavior, its ease of measurement and persistence, and its potential role in tree mortality, char height can be a valuable post-fire measurement for understanding tree mortality (see review in Fowler and Seig 2004).

Canopy scorch was a predictor of longleaf pine mortality in our nested logistic regression and has been associated with post-fire mortality in many other conifers (Peterson and Arbaugh 1986, Wyant et al. 1986, Ryan et al. 1988, Menges and Deyrup 2001, Stephens and Finney 2002). Our logistic regression models nested by treatment (dry, moist, wet burns) revealed that the role of scorch was confined to only the dry treatment, a potential explanation for the contradictory results found in restoration burns in which scorch was prevalent and a good predictor of mortality (Menges and Deyrup 2001), or was absent altogether and therefore not related to mortality in others (Kush et al. 2004, Varner and Kush 2004). This finding is critical in that it highlights the problem that exists in understanding fire effects with an often incomplete understanding of fuel or fire behavior characteristics that resulted in the observed effects. Understanding the dynamic role of canopy scorch in tree mortality will require a more mechanistic approach that includes isolation of scorch from other types of fire damage.

Given that duff consumption due to smoldering combustion was the only fire effect consistently related to pine mortality across scales and treatments (Tables 2-6), it seems worth closer consideration. In a model of factors that predict duff consumption, Oa percent fuel moisture explained 78% of variation in duff consumption (Table 7). In other coniferous forests, moisture content has long been recognized as a strong predictor duff consumption (Frandsen 1987, Brown et al. 1991, Ottmar et al. 1991, Sandberg et al. 2001). Duff is consumed by smoldering combustion, causing long-duration heating to stems and organic and mineral soil (Swezy and Agee 1991, Hungerford et al. 1995). The long duration (often hours post-ignition) of moderately elevated soil temperatures can damage or kill roots (Swezy and Agee 1991) and stem vascular tissues (Ryan and Frandsen 1991).

This study reinforces the need for a better understanding of the mechanisms by which fires kill trees (Dickinson and Johnson 2001, Kelsey and Joseph 2003, Fowler and Seig 2004). Future work on fire-caused mortality should isolate the different types of fire damage (see Carter et al. 2004, Fowler and Seig 2004) and consider their interactions (e.g., heat from smoldering duff damages vascular tissues in surficial roots and surrounding tree stems and renders trees susceptible to beetle attack). Such studies should combine whole tree physiology models with considerations of fire damage and subsequent increases in tree stress (Manion 1991, Dunn and Lorio 1992, Ryan 2000, Kelsey and Joseph 2003, Wallin et al. 2003).

Challenges to restoration and management using fire

Duff moisture content is controlled by several factors acting at different scales. At large scales, duff moisture is controlled by recent precipitation amounts and temporal distributions (Ferguson et al. 2002). Within stands, localized duff moisture can vary with forest floor composition, beneath and between tree crowns, and at small scales in basal duff accumulations (Gordon and Varner 2002, Miyanishi and Johnson 2002). Duff fuel particles vary in their physical and chemical composition (e.g., suberin-rich bark in contrast to extractive and cellulose-dominated pine needle litter), both of which affect ignition and burning characteristics at small scales.

Burning prescriptions for long-unburned forests will continue to require consideration of traditional synoptic weather variables but should be enhanced to acknowledge the important role of the novel forest floor fuel complex. Prescriptions should incorporate more robust estimates of time and duration of localized precipitation and drying, duff moisture (Ferguson et al. 2002), and the subsequent effects of these factors on fire behavior, particularly residence time (Frandsen 1987, Frandsen 1991, Miyanishi 2001, Miyanishi and Johnson 2002). Given that forest floor fuels in long-unburned longleaf pine forests are diverse in composition and structure, the drying, wetting, and burning behavior of this fuel complex warrants further study.

Prescriptions for fire reintroduction in long-unburned forests should be tailored to local operational scales. For example, it may be operationally feasible to use a combination of wetting (either with backpack or tractor-mounted units) and/or raking away forest floor fuels to minimize potential for long-duration heat damage to high-value trees in small stands. Pre-fire raking has been used successfully in *P. ponderosa* burning (e.g., Feeney et al. 1998, Wallin et al. 2002) but apparently less often in longleaf pine forests perhaps because it is labor-intensive and a few managers have reported what they believe to be raking-induced mortality (Varner and Kush 2004). Extinguishing smoldering duff fires with tractor or backpack-mounted water or foam has been successfully employed in small (< 20 ha) restoration fires (Kush et al. 2004). Unfortunately, none of these labor-intensive treatments are appropriate for large-scale restoration burning. Managers of large forests throughout the southeastern USA are faced with burning large areas with limited staffing and increasing limitations on smoke production (Hiers et al. 2003). For large areas, utilizing duff moisture and optimizing burn resources to priority stands must be the rule. In these situations, acceptable thresholds of tree mortality must be balanced with duff and woody fuel consumption and placed in the context of landscape objectives.

In restoration fires, managers and forest and fire scientists must recognize the increasingly important role of forest floor fuels and the unintended damage they can cause. Traditional fire effects such as canopy scorch and stem char are readily observed and modeled. In contrast, the same relationships between forest floor or duff consumption and overstory mortality are mostly speculative and lack widespread experimental support. The reason for this oversight may be that this phenomenon is rare but getting more common as fires are being reintroduced after long periods of suppression (e.g., Ryan and Frandsen 1991, Swezy and Agee 1991, Haase and Sackett 1995, Stephens and Finney 2002, McHugh and Kolb 2003). Land managers are still left with the conundrum of having to reduce duff fuels while maintaining a living overstory. Incorporating fuel moisture thresholds in burn prescriptions that include measures of the forest floor fuel complex may help managers avoid widespread overstory tree damage and mortality and successfully reduce fuels when they reintroduce fires after long periods of suppression.

Acknowledgements
This study was supported by funding from the Joint Fire Sciences Program through the USDA Forest Service Southern Research Station. We appreciate the support of Eglin Air Force Base Jackson Guard and the School of Natural Resources and the Environment at the University of Florida. H.L. Jerkins, K. Mock, J. Furman, D. Wright, C. Wright, C. Bolen, and C. Raymond assisted with experimental prescribed fires. We thank D. Wright, D. Olson, C. Wright, C. Bolen, C. Raymond, J. McCormick, and J. Mathey for fuel sampling. Field and lab assistance was provided by S. Wheeler, E. Owens, H.L. Jerkins, K. Mock, A. Sutsko, D. Grow, and B. Williams. Helpful comments on study design, implementation, and analysis were contributed by T. Martin, A. Long, D. Wade, and B. Vihnanek.

References

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

Agee, J.K. 2002. The fallacy of passive management. Cons. Biology in Action **3**: 18-25.

Barton, A.M. 2002. Intense wildfire in southeastern Arizona: transformation of a Madrean oak-pine forest to oak woodland. For. Ecol. and Manage. **165**: 205-212.

Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA For. Serv. Gen. Tech. Rep. INT-16.

Brown, J.K., Reinhardt, E.D., and Fischer, W.C. 1991. Predicting duff and woody fuel consumption in northern Idaho prescribed fires. For. Sci. **37**: 1550-1566.

Brown, R.L., Stone, E.L., and V.W. Carlisle. 1990. Soils. *In* Ecosystems of Florida. *Edited by* R.L. Myers and J. Ewel. University of Florida Presses, Gainesville.

Busse, M.D., Simon, S.A., and Rigel, G.M. 2000. Tree-growth and understory responses to low-severity prescribed burning in thinned Pinus ponderosa forests of central Oregon. For. Sci. **46**: 258-268.

Carter D.C., Hendricks J.J., Mitchell R.J., and Pecot S.D. 2004. Fine root carbon allocation and fates in longleaf pine forests. For. Sci. **50**: 177-187.

Christensen, N. L. 1981. Fire regimes in southeastern ecosystems. *In* Fire regimes and ecosystem properties. *Edited by* H.A. Mooney, T.M. Bonnicksen, N. L. Christensen, J.E. Lotan, and W.A. Reiners. U.S. For. Serv. Gen. Tech. Rep. GTR-WO-26. pp.112-136.

Covington, W. W. and Moore, M. M. 1994. Southwestern ponderosa forest structure: Changes since Euro-American settlement. Journal of Forestry **92**: 39-47.

Covington, W.W., Fulé, P.Z, Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S., and Wagner, M.R. 1997. Restoration of ecosystem health in southwestern ponderosa pine forests. J. For. **95**: 23-29.

Dickinson, M.B., and Johnson, E.A. 2001. Fire effects on trees. *In* Forest Fires: Behavior and Ecological Effects. *Edited by* E.A. Johnson and K. Miyanishi. Academic Press, San Diego, CA.

Dixon, W.N., Corneil, J.A., Wilkinson, R.C., and Foltz, J.L.1984. Using stem char to predict mortality and insect infestation of fire-damaged slash pines. South. J. Appl. For. **8**: 85-88.

Dunn, J.P., and Lorio, P.L.1992. Effects of bark girdling on carbohydrate supply and resistance of loblolly pine to southern pine beetle (*Dendroctonus frontalis* Zimm.) attack. For. Ecol. Manage. **50**: 317-330.

Elliott K.J., Vose, J.M. and Clinton, B.D. 2002. Growth of eastern white pine (*Pinus strobus* L.) related to forest floor consumption by prescribed fire in the southern Appalachians. So. J. Appl. For. **26**: 18-25.

Everett, R.L, Schellhaas, R., Keenum, D., Spurbeck, D., and Ohlson, P. 2000. Fire history of the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. For. Ecol. Manage. **129**: 207-225.

Feeney, S.R., Kolb, T. E., Covington, W.W., and Wagner, M.R.1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson Natural Area. Can. J. For. Res. **28**: 1295-1306.

Ferguson, S.A., Ruthford, J.E., McKay, S.J., Wright, D., Wright, C., and Ottmar, R. 2002. Measuring moisture dynamics to predict fire severity in longleaf pine forests. Intern. Journ. Wildl. Fire **11**: 267-279.

Fowler, J.F., and Sieg, C.H. 2004. Postfire mortality of ponderosa pine and Douglas-fir: a review of methods to predict tree death. USDA For. Serv. Gen. Tech. Rep. RMRS-132.

Frandsen, W.H. 1987. The influence of moisture and mineral soil on the combustion limits of smoldering forest duff. Can. J. For. Res. **17**: 1540-1544.

Frandsen, W.H. 1991. Burning rate of smoldering peat. Northwest Sci. **65**: 166-172.

Frost, C.C. 1993. Four centuries of changing landscape patterns in the longleaf pine ecosystem. Proc. Tall Timbers Fire Ecol. Conf. **18**:17-43.

Fulé, P.Z., Cocke, A.E., Heinlein, T.A., and Covington, W.W. 2004. Effects of an intense prescribed forest fire: is it ecological restoration? Rest. Ecol. **12**:220-230.

Gilliam, F.S., and Platt, W.J. 1999. Effects of long-term fire exclusion on tree species composition and stand structure in an old-growth *Pinus palustris* (longleaf pine) forest. Plant Ecol. **140**: 15-26.

Gordon, D.R., and Varner, J.M. 2002. Old-growth longleaf pine restoration and management. Final Report to Eglin Air Force Base Jackson Guard, Niceville, Fla. 33 pp.

Haase, S.M., and Sackett, S.S. 1998. Effects of prescribed fire in giant sequoia-mixed conifer stands in Sequoia and Kings Canyon National Parks. Proc. Tall Timbers Fire Ecol. Conf. **20**: 236-243.

Hermann, S.M. 1993. The longleaf pine ecosystem: ecology, restoration and management. Proc. Tall Timbers Fire Ecol. Conf. Tall Timbers Res. Sta., Tallahassee, FL.

Heyward, F. 1939. The relation of fire to stand composition of longleaf pine forests. Ecology **20**: 287-304.

Hiers, J.K., Laine, S.C., Bachant, J.J., Furman, J.H., Greene, W.W., and Compton, V. 2003. Simple spatial modeling

tool for prioritizing prescribed burning activities at the landscape scale. Cons. Biol. **17**: 1571-1578.
Hungerford, R.D., Frandsen, W.H., and Ryan, K.C. 1995. Ignition and burning characteristics of organic soils. Proc. Tall Timbers Fire Ecol. Conf. **19**: 78-91.
Johansen, R.W., and Wade, D.D. 1987. Effects of crown scorch on survival and diameter growth of slash pines. So. J. Appl. For. **11**: 180-184.
Johnson, E.A., and Miyanishi, K. 1995. The need for consideration of fire behavior and effects in prescribed burning. Rest. Ecol. **3**: 271-278.
Johnson, R., and Gjerstad, D.H. 1998. Landscape-scale restoration of the longleaf ecosystem. Rest. Manage. Notes **16**: 41-45.
Keane, R.E., Ryan, K.C., Veblen, T.T., Allen, C.D., Logan, J., and Hawkes, B. 2002. Cascading effects of fire exclusion in Rocky Mountain ecosystems: A literature review. USDA For. Serv. Gen. Tech. Rep. RMRS-91.
Kelsey, R.G., and Joseph, G. 2003. Ethanol in ponderosa pine as an indicator of physiological injury from fire and its relationship to secondary beetles. Can. J. For. Res. **33**: 870-884.
Kush, J.S., R.S. Meldahl, and C. Avery. 2004. A restoration success: longleaf pine seedlings established in a fire-suppressed, old-growth stand. Ecological Restoration **22:** 6-10.
Landers, J.L., van Lear, D.H., and Boyer, W.D. 1995. The longleaf pine forests of the southeast: requiem or renaissance? J. For. **93**: 39-44.
Manion, P.D. 1991. Tree disease concepts. Prentice-Hall, New Jersey.
Martin, R.E. 1963. A basic approach to fire injury of tree stems. Proc. Tall. Timbers Fire Ecol. Conf. **2**: 151-162.
McHugh, C.W., and Kolb, T.E.2003. Ponderosa pine mortality following fire in northern Arizona. Intern. Journ. Wildl. Fire 12:1-16.
Minnich, R.A. with M.G. Barbour, J.H. Burk and R.F. Fernav . 1995. Sixty years of change in conifer forests of the San Bernardino Mountains: Reconstruction of California mixed conifer forests prior to fire suppression. Cons. Biol. **9**: 902-914.
Menges, E.S., and Deyrup, M.A. 2001. Postfire survival in south Florida slash pine: Interacting effects of fire intensity, fire season, vegetation, burn size, and bark beetles. Intern. Journ. Wildl. Fire **10**: 53-63.
Miyanishi, K. 2001. Duff consumption. *In* Forest Fires: Behavior and Ecological Effects. *Edited by* E.A. Johnson and K. Miyanishi. Academic Press, San Diego, CA.
Miyanishi, K. and Johnson, E.A. 2002. Process and patterns of duff consumption in the mixedwood boreal forest. Can. J. For. Res. **32**: 1285-1295.
Myers, R.L. 1990. Scrub and high pine. *In* Ecosystems of Florida. *Edited by* R.L. Myers and J.J. Ewel. University Presses of Florida, Gainesville.
Noss, R.F., LaRoe, E.T., and Scott, J. M. 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. USDI National Biol. Serv. Biol. Rep. 28.
O'Brien, J.J., Ferguson, S.A, Hiers, J.K., and Ottmar, R.D. Weather and climatic influences on duff moisture and consumption in fire-excluded longleaf pine forests in Florida, USA. In prep.
Ostrosina, W.J., Hess, N.J., Zarnoch, S.J., Perry, T.J., and Jones, J.P. 1997. Blue-stain fungi associated with roots of southern pine trees attacked by the southern pine beetle, *Dendroctonus frontalis*. Plant Disease **81**:942-945.
Ostrosina, W.J., Bannwart, D., and Roncadori, R.W. 1999. Root-infecting fungi associated with a decline of longleaf pine in the southeastern United States. Plant and Soil **27**:145-150.
Ottmar, R.D., Burns, M.F., Hall, J.N., and Hanson, A.D. 1993. CONSUME user's guide. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-304.
Ottmar, R.D, Alvarado, E., and Hessburg, P.F. 1998. Linking recent historical and current forest vegetation patterns to smoke and crown fire in the Interior Columbia River Basin. *In* Proceedings of the 13th Conference on Fire and Forest Meteorology. *Edited by* R. Weber. Moran, WY: International Association of Wildland Fire.
Outcalt, K.W. 2000. Occurrence of fire in longleaf pine stands in the southeast United States. Proc. Tall Timbers Fire Ecol. Conf. **21**: 178-182.
Overing, J.D., Weeks, H.H., Wilson, J.P., Sullivan, J., and Ford, R.D. 1995. Soil Survey of Okaloosa County, Florida. USDA Natural Resource Conservation Service, Washington, D.C.
Peterson, D.L., and Arbaugh, M.J. 1986. Postfire survival in Douglas-fir and lodgepole pine: comparing effects of crown and bole damage. Can. J. For. Res. 16: 1175-1179.
Peterson, D.L., and Ryan, K.C. 1986. Modeling post-fire conifer mortality for long-range planning. Environ. Manage. 10: 797-806.
Robbins, L. E. and Myers, R.L.1992. Seasonal effects of prescribed burning in Florida: A review. Misc. Pub. No. 8, Tall Timbers Research Sta. 96 pp.
Ryan, K.C. 2000. Effects of fire injury on water relations of ponderosa pine. Proc. Tall Timbers Fire Ecol. Conf.**21**:

58-66.
Ryan, K.C., and Frandsen, W.H. 1991. Basal injury from smoldering fires in mature Pinus ponderosa Laws. Intern. Journ. Wildl. Fire **1**:107-118.
Ryan, K.C., Peterson, D.L., and Rheinhardt, E.D.1988. Modeling long-term fire-caused mortality of Douglas-fir. For. Sci. **34**: 190-199.
Ryan, K.C., and Rheinhardt, E.D. 1988. Predicting postfire mortality of seven western conifers. Can. J. For. Res. **18**: 1291-1297.
Sandberg, D.V., Ottmar, R.D., and Cushon, G.H. 2001. Characterizing fuels in the 21st century. Intern. Journ. Wildl. Fire **10**: 381-387.
Stephens, S.L., and Finney, M.A. 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. For. Ecol. Manage. **162**: 261-271.
Swezy, D.M., and Agee, J.K. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Can. J. For. Res. **21**: 626-634.
van Wagner, C.E. 1973. Height of crown scorch in forest fires. Can. J. For. Res. **3**: 373-378.
van Wagtendonk, J.W. 1985. Fire suppression effects on fuels and succession in short-fire-interval wilderness ecosystems. *In* Proceedings of a symposium and workshop on wilderness fire. *Edited by* J.E. Lotan, B.M. Kilgore, W.C. Fischer, and R.W. Mutch. U.S. For. Serv. Gen. Tech. Rep. GTR-INT-182. pp.119-126.
Varner, J.M., Kush, J.S., and Meldahl, R.S. 2000. Ecological restoration of an old-growth longleaf pine stand utilizing prescribed fire. Proc. Tall Timbers Fire Ecol. Conf. **21**: 216-219.
Varner, J.M., and Kush, J.S. 2004. Old-growth longleaf pine forests and savannas of the southeastern USA: status and trends. Nat. Areas J. **24**: 141-149.
Varner, J.M., D.R. Gordon, F.E. Putz, and J.K. Hiers. 2005. Restoring fire to long-unburned *Pinus palustris* ecosystems: novel fire effects and consequences for long-unburned ecosystems. Rest. Ecol. **13**: 1-9
Wade, D.D., and Johansen, R.W. 1986. Effects of fire on southern pine: observations and recommendations. USDA For. Serv. Gen. Tech. Rep. SE-41.
Wade, D.D. and Johansen, R.W. 1987. Relating wildland fire to defoliation and mortality in pine. *In* Proc. 4th Biennial So. Silv. Conf. *Edited by* D.R. Phillips. U.S. For. Serv. Gen. Tech. Rep. SE-42. pp. 107-110.
Wade, D.D., and Lunsford, J.D. 1989. A guide for prescribed fire in southern forests. USDA For. Serv. Tech. Pub. SRS-11.
Wade, D.D., Custer, G., Thorsen, J., Kaskey, P., Kush, J., Twomey, B., and Voltolina, D. 1997. Reintroduction of fire into fire-dependent ecosystems: some southern examples. Proc. Tall Timbers Fire Ecol. Conf. **20**: 94-98.
Wallin, K. F., T. E. Kolb, K. R. Skov, and M. R. Wagner. 2004. Seven-year results of thinning and burning restoration treatments on old ponderosa pines at the Gus Pearson Natural Area. Rest. Ecol. **12:**239-247.
Ware, S., Frost, C.C., and Doerr, P.D. 1993. Southern mixed hardwood forest: the former longleaf pine forest. *In* Biodiversity of the southeastern United States: lowland terrestrial communities. *Edited by* W.H., Martin, S.G. Boyce, and A.C. Echternacht. Wiley, New York.
Wright, C.S., and Agee, J.K. 2004. Fire and vegetation history in the eastern Cascade Mountains, Washington. Ecol. Appl. **14**: 443-459.
Wyant, J.G., Omi, P.N., and Laven, R.D. 1986. Fire-induced tree mortality in a Colorado ponderosa pine / Douglas-fir stand. For. Sci. **32**: 49-59.

Figures

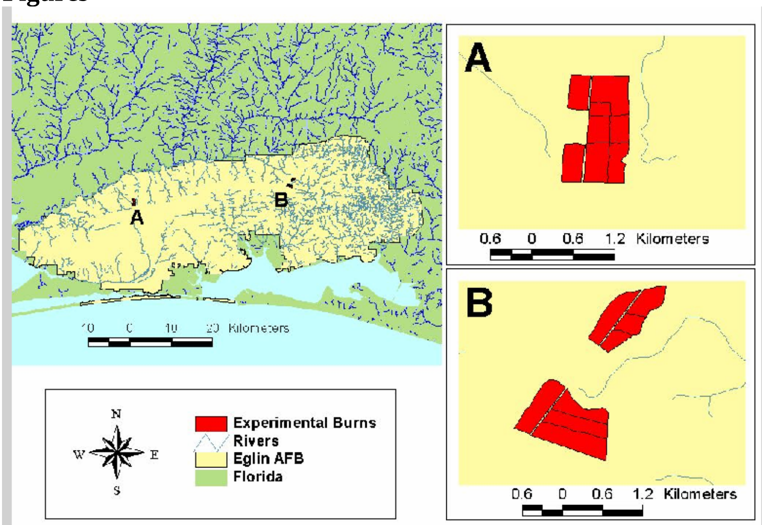


Figure 1. Study site locations of experimental prescribed fires to examine correlates of mortality resulting from reintroduction of fire into fire-suppressed (ca. 35 – 45 years since fire) longleaf pine (*Pinus palustris*) forests.

Figure 2. Photograph of typical long-unburned longleaf pine forest at Eglin Air Force Base, Florida, USA. With large-scale fire suppression, southeastern USA pinelands have altered structure, composition, and fuel characteristics (Louis Provencher photograph).

Figure 3. *In preparation* Treatment results –

Mortality v Treatment

Mortality v Char

Mortality v Scorch (%)

Mortality v Duff Consumption

Figure 4. Analysis of variance results for treatment effects of duff moisture on longleaf pine tree mortality.

log Pine Mortality (%)	Treatment Duff Moisture Content	10.56	12	0.001

Table 1. Fire weather and fuel moisture values for each experimental prescribed burn in long-unburned longleaf pine forests at Eglin Air Force Base in northern Florida, USA.

Site	Treatment[1]	Burn date	Rel. Hum. (%)	Air Temp. (°C)	Wind Speed (m sec^{-1})	Fuel Moisture Content (% dry wt.)[2] Oi	Oe	Oa	10-hr	100-hr	1000-hr[3]
RT01	Wet	Feb 18/01	26	17	0.45	18	69	102	26	54	83
RT02	Wet	Mar 05/02	24	12	0.89	27	70	125	43	61	--
RCX	Wet	Mar 14/02	64	20	1.34	22	76	133	42	45	77
RCM	Wet	Mar 04/02	21	8	0.89	35	91	137	52	66	86
	Wet *Treatment Means*		**34 A**[4]	**14 A**	**0.89 A**	**26 A**	**76 A**	**124 A**	**41 A**	**57 A**	**82 A**
RT01	Moist	Mar 27/01	24	16	0.45	14	41	117	20	44	119
RT02	Moist	Feb 22/02	43	17	1.34	17	43	79	25	45	--
RCX	Moist	Mar 08/02	35	24	1.79	16	45	112	22	28	70
RCM	Moist	Feb 22/02	37	18	0.45	14	27	102	18	39	64
	Moist *Treatment Means*		**35 A**	**19 AB**	**1.01 A**	**15 B**	**39 B**	**103 A**	**21 B**	**39 B**	**84 A**
RT01	Dry	Apr 26/01	43	32	0.45	16	18	40	18	15	92
RT02	Dry	Mar 24/02	39	23	0.89	12	27	87	13	22	--
RCX	Dry	Apr 07/02	60	19	1.34	11	46	64	9	13	33
RCM	Dry	Apr 24/02	53	28	0.89	7	11	59	14	18	47
	Dry *Treatment Means*		**49 A**	**26 B**	**0.89 A**	**12 B**	**26 B**	**62 B**	**14 B**	**17 C**	**57 A**

[1] Prescribed fire treatments were based on day-of-burn volumetric duff moisture content.
[2] Fuel moisture content for each fuel category was calculated based on day-of-burn collections of 5 samples per fuel category.
[3] 1000-hour fuel moisture contents are based on an average of both sound and rotten downed fuels (R. Ottmar, unpublished data).
[4] Different letters following treatment means denote significant differences among column means determined with ANOVA followed by post-hoc Tukey's HSD with $\alpha = 0.05$.

Table 2. Effects of prescribed burns in long-unburned longleaf pine forests at Eglin Air Force Base in northern Florida, USA. Values in columns are plot means, with standard deviations noted parenthetically.

Site	Treatment[1]	Basal Forest Floor Consumption				Stem Char	Canopy Scorch		Pine Mortality[2]
		Forest Floor		Duff					
		cm loss	% loss	cm loss	% loss	m	m height	% SC	%
RT01	Wet	1.3 (1.0)	24 (8)	0.2 (0.3)	2 (4)	1.0 (0.6)	--	--	0
RT02	Wet	3.7 (2.3)	33 (15)	0.5 (1.3)	5 (15)	1.4 (0.8)	4.5 (5.6)	5.8 (11.3)	0
RCX	Wet	3.2 (2.3)	33 (13)	0.3 (1.3)	4 (13)	0.9 (1.7)	4.1 (4.2)	4.3 (5.2)	0
RCM	Wet	7.9 (4.9)	49 (14)	1.2 (2.9)	9 (17)	2.1 (1.4)	10.3 (6.1)	23.6 (26.7)	2
	Wet *Treatment Means*	**4.0**	**35 A**[3]	**0.6**	**5 A**	**1.4 A**	**6.3**	**11.2 A**	**0.5 A**
RT01	Moist	3.4 (3.2)	28 (17)	0.9 (1.8)	9 (17)	1.2 (1.0)	--	--	0
RT02	Moist	3.3 (2.8)	31 (19)	1.0 (2.2)	11 (20)	1.0 (0.8)	3.5 (4.3)	8.8 (15.4)	4
RCX	Moist	7.8 (5.0)	52 (16)	2.3 (2.7)	22 (20)	3.1 (1.5)	10.2 (4.7)	35.9 (32.7)	6
RCM	Moist	7.4 (4.7)	56 (16)	1.4 (3.0)	16 (23)	5.1 (2.8)	16.7 (3.4)	71.7 (29.7)	2
	Moist *Treatment Means*	**5.5**	**42 A**	**1.4**	**14.5 A**	**2.6 A**	**10.1**	**38.8 A**	**3.0 A**
RT01	Dry	10.3 (4.7)	73 (26)	6.2 (4.0)	63 (34)	1.2 (1.0)	--	--	22
RT02	Dry	6.9 (3.2)	63 (14)	1.6 (2.0)	25 (23)	2.8 (1.6)	8.4 (6.3)	34.3 (36.6)	10
RCX	Dry	6.7 (3.6)	72 (11)	2.8 (2.6)	49 (18)	3.1 (1.4)	11.9 (3.1)	58.4 (31.4)	8
RCM	Dry	9.6 (5.0)	73 (17)	4.6 (3.9)	49 (27)	4.1 (2.2)	15.3 (3.7)	70.4 (33.7)	42
	Dry *Treatment Means*	**8.4**	**70 B**	**3.8**	**46.5 B**	**2.8 A**	**11.9**	**54.4 A**	**20.5 B**

[1] Prescribed fire treatments were based on day-of-burn volumetric duff moisture content.
[2] Percent tree mortality is cumulative mortality of all pines > 15 cm dbh. Mortality values for 2001 burns include surveys 36 months post-burn; mortality values for all 2002 burns include surveys 24 months post-burn.
[3] Different letters following treatment means denote significant differences among column means determined with ANOVA followed by post-hoc Tukey's HSD with $\alpha = 0.05$.

Table 3. Univariate linear regression results for correlates of individual pine mortality resulting from prescribed restoration burns in long-unburned forests at Eglin Air Force Base in northern Florida, USA.

Dependent Variable	Independent Variable	R^2	*P*
Day-of-Burn Variables			
log Pine Mortality (%)	Ambient Air Temperature (C)	0.36	0.04
log Pine Mortality (%)	Relative Humidity (%)	0.11	0.30
log Pine Mortality (%)	10-hour Fuel Moisture (%)	0.26	0.09
log Pine Mortality (%)	100-hour Fuel Moisture (%)	0.47	0.01
log Pine Mortality (%)	1000-hour Fuel Moisture (%)	0.31	0.12
log Pine Mortality (%)	Oi (litter horizon) Fuel Moisture (%)	0.17	0.19
log Pine Mortality (%)	Oe (fermentation horizon) Fuel Moisture (%)	0.36	0.04
log Pine Mortality (%)	Oa (humus horizon) Fuel Moisture (%)	0.50	0.01
Fire Effects Variables			
log Pine Mortality (%)	Forest Floor (litter+duff) Reduction (%)	0.71	<0.001
log Pine Mortality (%)	Duff Reduction (%)	0.57	0.04
log Pine Mortality (%)	Canopy Scorch Volume (%)	0.43	0.06
log Pine Mortality (%)	Stem Char Height (m)	0.38	0.03

Table 4. Step-wise multiple regression results for predictors of stand longleaf pine mortality caused by prescribed restoration burns in long-unburned pinelands at Eglin Air Force Base in northern Florida, USA.

Dependent Variable	Parameters $ß_0$	$ß_1$	R^2	P	AIC [1]
Fuel Environment Variables					
log Pine Mortality (%) =	6.26	- 0.07 (Oa% moisture)	.45	0.04	19.8
Fire Effects Variables					
log Pine Mortality (%) =	-2.24	+ 0.12 (% duff reduction)	.52	0.03	15.9
Combined Model (Fuel Environment + Fire Effects)					
log Pine Mortality (%) =	-2.93	+ 0.15 (% duff reduction)	.57	< 0.01	5.1

[1] AIC (Akaike's Information Criteria) values rank competing regression models; models with lower AIC values approximate modeled responses better than models with higher AIC values.

Table 5. Modeled logistic regression of post-fire individual tree longleaf pine mortality at Eglin Air Force Base in northern Florida, USA.

Dependent Variable	$ß_0$	$ß_1$	$ß_2$	χ^2	R^2	P
Tree Status (alive/dead) =	4.79	- 0.02 (% scorch)	- 0.04 (% duff reduction)	87.4	.31	<.0001

Table 6. Modeled nested logistic regression of post-fire individual tree longleaf pine mortality at Eglin Air Force Base in northern Florida, USA.

Fire Effects Nested within Treatments		Parameter Estimate	χ^2	*P*	R^2
Tree Status (alive/dead)					
Intercept		3.16	21.29	<0.001	
Dry Treatment	% Canopy Scorch	-0.03	11.65	<0.001	
Moist Treatment	% Canopy Scorch	-0.01	0.32	0.57	
Wet Treatment	% Canopy Scorch	-0.03	1.39	0.24	
Dry Treatment	% Duff Consumption	-0.04	15.44	<0.001	
Moist Treatment	% Duff Consumption	-0.03	7.29	<0.01	
Wet Treatment	% Duff Consumption	-0.07	5.03	<0.01	
Whole Model			**96.35**	**<0.001**	**0.34**

Table 7. Modeled step-wise multiple regression of duff consumption resulting from restoration burns in long-unburned longleaf pine forests at Eglin Air Force Base in northern Florida, USA.

Dependent Variable	β_0	β_1	RMSE	R^2	*P*
Duff Consumption (%) =	78.6	- 0.59 (Oa % fuel moisture)	10.07	.78	<.0001

APPENDIX F.

Effects of basal bark, duff, and soil temperatures on tree stress and growth

J. Morgan Varner, III [1,2], Joseph J. O'Brien[3], Robert J. Mitchell[4], J. Kevin Hiers[5,7], Francis E. Putz [6], and Doria R. Gordon [6,7]

[1] School of Natural Resources and Environment, University of Florida, Gainesville, FL
[3] USDA Forest Service Southern Research Station, Athens, GA
[4] J. W. Jones Ecological Research Center, Newton, GA
[5] The Nature Conservancy, Thomasville, GA
[6] Department of Botany, University of Florida, Gainesville, FL
[7] The Nature Conservancy, Gainesville, FL

[2] **Corresponding author & present address (e-mail: jmvarner@humboldt.edu)**
J. Morgan Varner, III
Department of Forestry and Watershed Management
Humboldt State University
1 Harpst Street
Arcata, CA 95521, U.S.A.
(707) 826-5622 Tel.
(707) 826-5634 Fax.

ABSTRACT
Understanding the proximate causes of post-fire conifer mortality associated with smoldering duff is a pressing issue for restoration and management of coniferous forests throughout North America. The primary causes for duff fire-mortality phenomenon are debated, but to date lack experimentation. We burned 80 mature *Pinus palustris* in a randomized experiment testing the effects of basal burning treatments (long-duration heating to stem vascular meristems, surficial roots, combinations of the two, and a non-smoldering control) and lethal temperature durations on subsequent pine radial growth and root nonstructural carbohydrates. Duff and mineral soil temperatures in the experimental fires were consistently above lethal temperatures (> 60º C) for hours following ignition, with values above 60º C recorded to 20 cm below the mineral soil surface. Post-fire changes in radial growth were related to duration of temperatures > 60º C in the upper 5-cm of mineral soil ($P = 0.08$) and changes in latewood increment in the year following fires was related to duration of temperatures > 60º C at 10-cm depths within the mineral soil ($P = 0.05$), but neither explained much of the variability in post-fire growth ($R^2 = 0.16$ and 0.17 for radial and latewood growth, respectively). In contrast, changes 120 days following burning in nonstructural carbohydrate content in coarse roots (2-5 mm diameter) were strongly linked to 5-cm mineral soil heating duration ($P<0.01$; $R^2 = 0.59$). Results from this study implicate the role of mineral soil heating, not basal girdling, in the post-fire decline of longleaf pine.

Keywords: ecological restoration, nonstructural carbohydrates, pine mortality, smoldering duff, soil heating.

INTRODUCTION

Fires, while pervasive elements of many coniferous forest landscapes, can stress, reduce growth, and kill "fire-adapted" conifers. Generating a stronger understanding of conifer mortality following fire is an increasingly important topic, given recent attempts to restore fire-excluded forests and manage the increasing area of post-wildfire forests in both the eastern and western USA (Wyant et al. 1986, Ryan and Reinhardt 1988, Ryan et al. 1988, Ryan and Frandsen 1991, Swezy and Agee 1991, Covington et al. 1997, Wade et al. 1997, Haase and Sackett 1998, Stephens and Finney 2002, McHugh and Kolb 2003, Agee 2003, Varner et al. 2005). Heat from surface, ground, and crown fires damage root, stem, and canopy meristems and cause stress that reduced tree defenses against pathogens or weather periodic climatic stress (Feeney et al. 1998, Kolb et al. 1998, McHugh et al. 2003). A major stumbling block in our understanding of post-fire tree mortality has been ascertaining causes and linkages between fuel, fire behavior, and its influence on post-fire stress and mortality.

The causes of post-fire conifer mortality are complicated and debated, but critical to the management of fire, fuels, and forest health. Fire damage to surface and duff-bound roots is a proposed cause of mortality in *P. ponderosa* (Swezy and Agee 1991). Stem vascular tissue death also results from fires in *P. ponderosa* (Ryan and Frandsen 1991, Ryan 2000). Canopy scorch has been linked to post-fire mortality of *P. elliottii* (Dixon et al. 1984, Wade and Johansen 1987, Menges and Deyrup 2001). Combinations of fire-caused damages appears likely to affect tree survival; indeed several investigators report the best predictors of post-fire mortality as those that include damages to multiple tissues (Wyant et al. 1986, Ryan and Reinhardt 1988, Ryan et al. 1988, Saveland and Neuenschwander 1990, Haase and Sackett 1998, Ryan 2000). Second-order fire effects such as bark beetle infestations (Dixon et al. 1984, Menges and Deyrup 2001, McHugh et al. 2003) and fungal diseases (Ostrosina et al. 1997, Ostrosina et al. 1999) are cited as causes of post-fire decline and mortality, but are likely linked to compromises in tree defenses caused by fire-caused damages to stem, canopy, or root tissues. The inability to establish a relationship among the responses of trees, the characteristics of the disturbing fire (i.e., temperatures, duration of lethal heating), and the fuels that fed them reduces our understanding of the ecology of fire as a disturbance, and inhibits restoration management of fire-excluded stands.

Stem damage has been simulated in individual tree experiments (Martin 1963, Hare 1964, Ryan 2000, van Mantgem and Schwartz 2004, Dickinson and Johnson 2004), as have fuels (Frandsen 1987, Frandsen 1991, Fonda 2001, Miyanishi and Johnson 2002, Fonda and Varner 2005), and soil temperatures (Frandsen and Ryan 1986, Steward et al. 1990). Replicating flaming fire experiments is hampered by the discontinuity in behavior and effects between small and large fires (Johnson and Miyanishi 1995). Small fires rarely coalesce to cause crown damage or fire intensities observed in large landscape fires. Smoldering fire, however, operates on such a small scale (1-100 cm^3 hr^{-1}) as to allow manipulative, replicated experimentation on individual trees and fuel microcosms (Frandsen 1987, Frandsen 1991, Miyanishi and Johnson 2002).

The objectives of this study were to link fuels and fire temperatures to specific damage, the subsequent growth, carbohydrate storage, and mortality of mature *Pinus palustris* in replicated small-scale burns. Specifically, we hypothesized that:

1. basal bark, duff, and surface mineral soil heating would be linked to proximal fuel moistures,
2. radial stem growth following burning would be related to type of damage, temperatures and duration of heating to basal bark, duff, and surface mineral soil, and
3. changes in root carbohydrate storage following burning would be related to type of damage, temperatures and duration of heating to basal bark, duff, and surface mineral soil.

This work is needed to inform regional restoration efforts (Varner et al. 2005) and to elucidate causes of post-fire conifer decline and mortality common throughout North American coniferous forests.

METHODS

Study Site

This experiment was conducted in a long-unburned (37 years since fire) longleaf pine stand at the Ordway-Swisher Memorial Preserve near Melrose, Florida, USA (N 29º 40', W 81º 74; Figure 1). The stand was dominated by an overstory of longleaf pine, with a thick midstory of oaks (*Quercus laevis, Q. geminata,* and *Q. hemisphaerica*), a patchy remnant groundcover dominated by *Aristida stricta*, and a thick forest floor (depths to 15 cm) typical of long-unburned xeric southeastern pine ecosystems (Varner et al. 2005). Soils of the site are deep, extensively well-drained hyperthermic, uncoated Lamellic Quartzipsamments in the Candler series (Readle 1990). The topography is gentle, with gentle north-facing slopes < 5% and elevations averaging 16 m above msl. The climate is humid, subtropical with long, warm, and humid summers and short, mild winters with annual temperatures and precipitation averaging 20º C and 1432 mm, respectively (Readle 1990).

One-m radius plots were established around each of 80 randomly selected mature (30 – 50 cm DBH) longleaf pine trees. In a completely randomized experiment, four treatments (20 replicates per treatment) were installed that include three hypothesized causes of post-fire mortality: 1) root damage (ROOT); 2) root and stem damage (ROOT+STEM); 3) stem damage (STEM); and 4) a control treatment that burned, but was extinguished prior to smoldering phase combustion (CONTROL). Root damage treatments were accomplished by allowing forest floor combustion while protecting the basal bark with fire retardant material (Cleveland Laminating Corp., Cleveland, OH, USA) sheathed over 15 cm high aluminum flashing embedded 10 cm from the basal bark (Figure 2). In the ROOT+STEM treatment, fires were allowed to heat both basal bark and duff and underlying roots. STEM treatments heated basal bark, with the adjacent forest floor protected with fire retardant material wrapped around embedded 15 cm high aluminum flashing. CONTROL burns were extinguished with a flapper once flaming fire subsided.

Tree measurements

Since mortality following basal damage is delayed in longleaf pines (Varner et al. 2005), two surrogates were used to approximate tree stress: radial growth (Busse et al. 2001) and root non-structural carbohydrates (Wargo et al. 1972, Marshall and Waring 1985, Kozlowski and Pallardy 1997). Radial stem growth (mm) of all 80 treatment trees was measured using increment cores (2 per tree, 90º apart) extracted one year post-burn (January-February 2005). Cores were air-dried, mounted, and sanded according to standard dendrochronological methodology (Stokes and Smiley 1968). All cores were measured using a binocular microscope with both earlywood and latewood measured to the nearest 0.01 mm.

Within a randomly selected subset of 8 trees in each burning treatment, we sampled total non-structural carbohydrate concentrations (starch + sugar) in roots immediately post-fire to document the carbon status of the tree within 10 days following burns and at 4 months post-burn (hereafter, "tnc_{10}" and "tnc_{120}"). For our tnc_{10} samples, we selected these trees within 10 days following the burn, a period that minimizes the transformations of the root carbohydrates from their pre-treatment carbohydrate status (Kozlowski and Pallardy 1997). For each of our root carbohydrate samples, we unearthed 3 g of fine (root diameter 1-2 mm) and 3 g of coarse (root diameter 2-5 mm) longleaf pine roots from the surficial mineral soil horizon surrounding burned trees. All roots were bagged and immediately stored on dry ice in the field, then transported to the laboratory within 8 hours. Immediately upon removal from chilling, the roots were rinsed and oven-dried at 100° C for 2 h, followed by drying at 70° C to a constant mass, minimizing post-harvest carbohydrate losses (Caldwell 1989).

Root non-structural carbohydrate samples were analyzed using a modified phenol-sulphuric acid method (Buysee and Merckx 1993). From each medium and coarse diameter dry root sample, 80 mg was extracted for 12 h in 10 mL 80% ethanol then centrifuged at 2200 rpm for 15 min. The resulting supernatant was removed and placed in a 50 mL flask. The residue was centrifuged a second time in 5 mL 80% ethanol solution for 5 min, and the supernatant was transferred to the same volumetric flask. The volume of the supernatant was adjusted to 50 mL and was used for the total sugar analysis. The residue from the ethanol extractions was transferred to a glass tube, dried, and subsequently boiled for 3 h in a 5 mL 3% HCl solution. The filtrate was adjusted to 50 mL in a volumetric flask and used for the starch analysis. For total sugar and starch determinations, 1 mL of a solution containing 20 to 80 µg sugar was transferred into a glass tube and 1 mL of a 28% phenol in 80% ethanol was added. Five mL of concentrated sulfuric acid was immediately added directly to the liquid surface. The tube was agitated for 1 min and allowed to stand for 15 min prior to measuring absorbance. Each sample was measured at 490 nm in a Shimadzu UV spectrophotometer (Shimadzu Corporation, Kyoto, Japan).

Basal forest floor

To understand the role of fuels on fire intensity and tree damage, we measured the basal forest floor consumption surrounding each treatment tree. Eight 20 cm tall steel pins were installed flush with the forest floor 8 cm from the stem in cardinal and ordinal directions. Following all burns, pins were measured for depth reduction [(initial depth - post-fire depth) / initial depth]. To estimate horizon moisture content, forest floor fuels were collected each burn day in by horizon from trees proximal to treatment trees. Samples were divided along horizons, with Oi removed first, then Oe material, concluding with Oa fuels. Since pine cones are likely vectors of duff ignition (Fonda and Varner 2005), six pine cones (3 recent, 3 decomposing) within the drip line of the source tree were collected and sealed in 4 mm polyethylene bags. In the laboratory, all fuels were oven-dried at 70° C to a constant weight to determine moisture content and dry biomass.

Fire Measurements

Fire temperatures were measured on a subset of all treatment trees during fires using Type J (range 0º to 1200° C) thermocouples connected to a Campbell Scientific CR10X datalogger. Temperature was measured on the bark surface at three points 120º apart at the forest floor-bark interface and at DBH (1 point). To assess root and soil heating, thermocouples were buried 120º apart in the lower duff (Oa horizon; 3 points), and directly beneath these points in the mineral soil at 5, 10, and 20 cm depths (9 points). Temperature was measured every two minutes from

15 minutes pre-ignition through the duration of the burning day (termination was required by 1700 hours on all burning days except the 4 November fire).

Each tree was ring-ignited with a drip torch from a 1 m raked line over a 34 day period beginning 25 September and concluding 4 November 2003. Time of ignition fuel moisture samples were collected from adjacent pines. During fire measurements included maximum flame height (cm), flame time (sec), and residual smoldering time (sec). Fire weather (wind speed, air temperature, and relative humidity) was recorded periodically during all fires (Table 1).

Following all burns, we measured forest floor consumption, bole char height, and canopy damage. Forest floor consumption was estimated by measuring the difference in pin exposure following fires. Stem char (bole char severity and char height) and any crown damage (scorch or consumption; unlikely in such small burn areas) were measured within two weeks post-burn.

Data analysis

The experiment was a completely randomized design with 4 fire treatments (ROOT, STEM, ROOT+STEM, CONTROL) with 20 replicates in each treatment. To detect treatment effects, we used ANOVA, with any differences among treatments determined using a post-hoc Tukey-Kramer HSD (with $\alpha = 0.05$ prior to analysis). We tested the effects of treatments on forest floor consumption (%), duration (minutes) of heating >60º C (lethal temperature; Byram 1958), 1-year radial growth (earlywood and latewood increment; mm), mortality (%), and changes in non-structural carbohydrates (fine and coarse; %) post-burn. In addition to the ANOVA, we used a step-wise multiple regression to examine relationships between fuel moistures (Oi, Oe, Oa, cone, 5 cm mineral soil) and weather with fire behavior and duration. Step-wise regressions were also used to relate heating duration in the different strata to tree mortality (%), 1-year radial growth (earlywood and latewood increment; mm), and changes in root non-structural carbohydrates (both fine and coarse diameters; %) post-burn. To meet assumptions of parametric analyses, any non-normal data were transformed prior to analysis according to convention (Zar 1996).

RESULTS

Fire narrative

Flame heights of the experimental burns ranged from 0.4 to 3.0 m (mean =1.52 m; s.d. = 0.70 m). No pines burned in this study experienced any canopy scorch. Fire temperatures during experimental burns were highest above-ground, with average maximum basal bark temperatures in individual fires ranging to 476º C, average duff temperatures to 304º C, and average mineral soil temperatures at 5-, 10-, and 20-cm below the surface to 134º, 117º, and 80º C (Table 2), respectively. These values are similar to those from other smoldering duff fires (Haase and Sackett 1998). Durations of heating above 60º C were longest in duff (mean = 74 ± 168.8 min), then on basal bark (mean = 36 ± 73.9 min), then decreased predictably with increasing mineral soil depth (27 ± 74.8, 7 ± 14.4, 1 ± 2.5 min at 5-, 10-, and 20-cm depths). Following ignition, increases in temperatures followed an expected pattern, with bark temperatures rising first, then duff, then sequential depths in the mineral soil (Figure 3a). The overnight burns (4 November) showed continued temperature rise in both duff and mineral soil strata (Figure 3b). As designed, basal bark temperatures were higher in ROOT+STEM and STEM treatments ($P=0.059$, df=3, $F= 2.91$). Duff and mineral soil temperatures at all depths, however, did not differ among treatments (Table 3). Average forest floor consumption differed among treatments ($P < 0.001$, df=3, $F= 6.69$; Table 3), with the ROOT+STEM treatment having the greatest fuel consumption. As expected, smoldering time also differed among burning treatments ($P= 0.018$, df=3, $F= 5.49$; Table 3), with all smoldering treatments (ROOT, ROOT+STEM, and STEM) differing from the control.

Temperatures on the basal bark and within the duff, and 5-, 10-, and 20-cm deep in the mineral soil were related to several fuel moisture parameters. In a step-wise regression with day-of-burn fuel moistures and weather observations, basal bark temperatures > 60º C were best predicted by lower duff (Oa horizon) moisture content ($P= 0.05$, $R^2= 0.16$). The best step-wise fit for duff temperatures > 60º C was a function of Oe moisture (fermentation horizon or "upper duff") moisture content ($P=0.01$, $R^2 = 0.24$). Among mineral soil temperature predictors, none were related to heating duration in the underlying mineral soil depths (5-, 10-, and 2-cm depths; Table 4). Heating duration among all strata (basal bark, duff, and 5-, 10-, and 20-cm mineral soil depths) were correlated (all $P < 0.05$). It follows that since the litter and duff fuels (Oi, Oe, and Oa horizons) were the source of heat for all strata, all strata were highly correlated with duff heating duration (bark: $r = 0.60$; 5-cm soil: $r = 0.76$; 10-cm soil: $r = 0.67$; and 20-cm soil: $r = 0.48$; all $P < 0.025$).

Radial Growth & Mortality

No pine mortality occurred during the first 10 months of the study, but there was significant variation in radial growth one-year following burning. Radial growth did not differ among treatments (P=0.58), but growth was related to heating duration across treatments. In a step-wise regression, radial growth loss (% change from 2003 ring radius) was related to heating duration > 60º C within the top 5 cm of mineral soil (P = 0.08, R^2 = 0.16; Table 5). Earlywood increment was insensitive to heating durations, but the step-wise model related latewood growth to 10-cm mineral soil temperatures > 60º C (P=0.069; R^2 = 0.17).

Carbohydrates

As with radial growth, root carbohydrates were not affected by fire treatments (Table 3). Heating durations across treatments, however, were related to root carbohydrate supplies. Fine (1-2 mm diameter) pine root carbohydrates were insensitive to heating durations (Table 5). Coarse pine root carbohydrates were affected by burning duration; heating > 60º C at 5 cm depths in the mineral soil was related to carbohydrate loss (P<0.01), explaining 59% of the variation in post-burn changes in coarse root carbohydrates (Table 5).

DISCUSSION

As has been reported for several North American conifers (e.g., Ryan 2000, Stephens and Finney 2002, Agee 2003, McHugh and Kolb 2003, Varner et al. 2005), we encountered no mortality within the first year following fire damage, likely due to "delayed mortality." The variation in post-burn radial growth during the first year following the fires was related (R^2 = 0.16) to heating duration > 60º C within the top 5 cm of mineral soil. Latewood increment was most closely linked to heating duration 10-cm below the mineral soil surface (Table 5), but again explained very little (R^2 = 0.16) of the variation in post-fire radial growth. From these radial growth results, we suggest that heat from mineral soil heating decreases radial growth in the year following fire. These data suggest a multiple damage (root and stem damage) cause of post-fire tree decline, but are confounded with autocorrelations among strata. Additionally, in contrast to the preceding years, the growth year 2004 was the wettest year in the last decade and within the terminating year of the longest sustained drought in northern Florida recorded history (National Climate Date Center 2005), potentially concealing or delaying the effects of damage.

Changes in root carbohydrates found in this study strongly support the role of mineral soil heating as the primary culprit of post-fire tree stress. Whereas stem radial growth in longleaf pine represents an aggregate of both the current and preceding year's stresses (Meldahl et al. 1999), carbohydrate supplies are metrics of current tree stress (Wargo et al. 1972, Marshall and Waring 1985, Dunn and Lorio 1992, Kozlowski and Pallardy 1997, Guo et al. 2004). Long duration lethal heating at 5 cm depths explained 59% of the variation in post-burn changes in coarse root carbohydrates (Table 5), support for root heating as a cause of overstory tree stress, and potentially the widespread mortality reported following restoration fires region-wide (Varner et al. 2005). As periodic post-burn surveys continue at this site, it will be interesting to compare this short-term (120 days post-burn) carbohydrate loss on its consequences for both subsequent radial growth (2005 and beyond) and pine mortality.

We found no treatment effect in this study; none of the damage treatments (ROOT, ROOT+STEM, STEM, or CONTROL) had an effect on either radial stem growth or root carbohydrate loss (Table 3). Heating duration across all treatments varied tremendously (Table 2), which most likely explains the lack of response. Future sampling will determine if the lack of effects was due to lags in growth (Meldahl et al. 1999, Busse et al. 2000) and mortality (Ryan 2000, Stephens and Finney 2002, Agee 2003, McHugh and Kolb 2003, Varner et al. 2005) reported in other post-fire studies. Additionally, the fact that all treatment pines were extinguished at 1700 EST daily (according to prescription) may have reduced the post-fire moisture stress often reported as a factor in post-fire tree stress (Ryan 2000).

Fire research is fraught with operational and statistical problems (van Mantgem and Schwartz 2001, McHugh and Kolb 2003); one problem with this experimental methodology was post-fire extinguishment. All treatments were extinguished with water according to prescription, with all attempts to minimize forest floor disturbance for post-burn fuel consumption measurements. Fires with sufficient intensity required additional watering, thereby providing those trees that were subjected to greater intensities with more post-fire water. This operational problem may have confounded results by alleviating some of the moisture stress associated with post-fire environments (Ryan 2000). Fire managers attest to the role of post-burn precipitation for modifying post-fire tree stress and mortality. This problem (role of post-fire water on subsequent growth and mortality) lends itself to future experimental work with meaningful field applications.

Among the most striking results from this experiment was the depth and duration of heating in the lower duff and mineral soil (Figure 3). Across all smoldering treatments, duff temperatures were elevated above ambient (23º C) temperatures. This finding is significant given that in long-unburned longleaf pine stands targeted for restoration, roughly half of all fine roots grow within basal duff (Gordon and Varner 2002) and the proximity of the underlying roots in the surface mineral soil (Heyward 1933). Mineral soil heating, the most prominent predictor of reductions in growth and stored carbohydrates, was above > 60º C in the top 5-cm in 58% of all burns (75% of treatments designed for root heating), as well as in lower depths: 42 and 25% of all burns propagated temperatures > 60 º C to depths of 10- and 20-cm below the surface, respectively. In the only overnight burn (4 November 2003; all other burns were extinguished according to prescription), temperatures in the mineral soil were maintained above lethal levels overnight (Figure 3), perhaps indicative of how other trees would have burned if not extinguished and how fuels smolder in actual fires.

Duff and soil heating, even at such short durations suggest significant root heating and fire-caused root mortality in smoldering fires. Prolonged heating will surely kill small pine roots, but may also damage or kill higher-order roots (Guo et al. 2004; Varner, *personal observation,* 2004) that connect large numbers of smaller roots to the tree, cascading localized effects into larger whole-tree damage. Given the strong findings linking root carbohydrate loss to soil heating duration, we can predict that prolonged smoldering would exacerbate post-fire stress and perhaps, mortality. We cannot say whether such root damage is the sole cause of tree decline and mortality, but the link between temperature duration and resulting stem radial growth and root carbohydrate drain underscore our need to better understand fire damage and the physiological response to fire-caused injury (Ryan 2000, Johnson and Miyanishi 2001).

Regardless of mechanism (root or basal damage), one major shortcoming in our understanding of smoldering fires is linking the fuel (basal duff) to the damage (tree damage). Basal duff is compositionally and structurally complex (Chapter 3), hence the determinants of its ignition, smoldering duration, and extinguishment are poorly understood. In this study, the best predictive model for duration of duff heating (Table 4) only explained 19% of the variation in this critical component. Given the importance of duff smoldering and its implications for conifer mortality throughout North America, future work should focus on better characterizing duff fuels, variation in their moisture content, and determinants of their ignition and combustion. With continued large scale fire exclusion in southeastern pine forests and in coniferous forests throughout North America, problems with duff smoldering will only increase.

Acknowledgments
This project was supported by funds provided to the USDA Forest Service, Southern Research Station, Asheville, North Carolina, from the Joint Fire Science Program of the Departments of Agriculture (Forest Service) and Interior (Bureau of Land Management). We appreciate the coordination and support of S. Coates and the Carl Swisher-Katharine Ordway Preserve and the University of Florida. E. Owens assisted with experimental fires and field data collection. Laboratory analysis was performed by E. Owens, D. Williams, D. Guo, and S. Pecot. Helpful comments on study design, implementation, and analysis were contributed by T. Martin, A. Long, N. Pederson, and B. Poulter.

LITERATURE CITED
Agee, J. K. 2003. Monitoring post-fire mortality in mixed-conifer forests of Crater Lake, Oregon. Natural Areas Journal 23:114-120.

Busse, M. D., S. A. Simon, and G. M. Riegel. 2000. Tree-growth and understory responses to low-severity prescribed burning in thinned *Pinus ponderosa* forests of central Oregon. Forest Science 46: 258-268.

Buysse, J. and R. Merckx. 1993. An improved colorimetric method to quantify sugar content of plant tissue. Journal of Experimental Botany 44: 1627-1629.

Byram, G. M. 1958. Some basic thermal processes controlling the effects of fire on living vegetation. USDA Forest Service Note SE-114. Southeastern Forest Exp. Station, New Orleans. 2 p.

Covington, W.W., P.Z. Fulé, M.M. Moore, S.C. Hart, T.E. Kolb, J.N. Mast, S.S. Sackett, and M.R. Wagner. 1997. Restoration of ecosystem health in southwestern ponderosa pine forests. Journal of Forestry 95:23-29.

Dickinson, M. B. and E. A Johnson. 2001. Fire effects on trees. Pages 477-525 *in*: Johnson, E. A. and K. Miyanishi, Eds. Forest Fires. Academic Press, New York.

Dickinson, M.B., and E.A. Johnson. 2004. Temperature-dependent rate models of vascular cambium cell mortality. Canadian Journal of Forest Research 34: 546-559.

Dixon, W. N., J. A. Corneil, R. C. Wilkinson, and J. L. Foltz. 1984. Using stem char to predict mortality and insect infestation of fire-damaged slash pines. Southern Journal of Applied Forestry 8:85-88.

Dunn, J. P. and P. L. Lorio, Jr. 1992. Effects of bark girdling on carbohydrate supply and resistance of loblolly pine to southern pine beetle (*Dendroctonus frontalis* Zimm.) attack. Forest Ecol. and Management 50:317-330.

Fahnestock, G. R. and R. C. Hare. 1964. Heating of tree trunks in surface fires. Journal of Forestry 62:799-805.

Feeney, S.R., T. E. Kolb, W.W. Covington, and M.R. Wagner. 1998. Influence of thinning and burning restoration treatments on presettlement ponderosa pines at the Gus Pearson Natural Area. Can. J. Forest Res. 28: 1295-1306.

Fonda, R.W. 2001. Burning characteristics of needles from eight pine species. Forest Science 47:390-396.

Fonda, R.W. and J.M. Varner. Burning characteristics of cones from eight pine species. Northwest Science 78: 322-333.

Frandsen, W. H. 1987. The influence of moisture and mineral soil on the combustion limits of smoldering forest duff. Canadian Journal of Forest Research 17: 1540-1544.

Frandsen, W. H. 1991. Burning rate of smoldering peat. Northwest Science 65: 166-172.

Frandsen, W.H., and K.C. Ryan. 1986. Soil moisture reduces belowground heat flux and soil temperatures under a burning fuel pile. Canadian Journal of Forest Research 16: 244-248.

Guo, D.L., Mitchell, R.J., and J.J. Hendricks. 2004. Fine root branch orders respond differentially to carbon source-sink manipulations in a longleaf pine forest. Oecologia 140:450-457.

Haase, S. M. and S.S. Sackett. 1998. Effects of prescribed fire in giant sequoia-mixed conifer stands in Sequoia and Kings Canyon National Parks. Tall Timbers Fire Ecology Conference Proceedings 20: 236-243. Tall Timbers Research Station, Tallahassee, FL.

Heyward, F. 1933. The root system of longleaf pine on the deep sands of western Florida. Ecology 14: 136-148.

Johansen, R.W. and D.D. Wade. 1987. Effects of crown scorch on survival and diameter growth of slash pines. Southern Journal of Applied Forestry 11: 180-4.

Johnson, E.A. and K. Miyanishi. 1995. The need for consideration of fire behavior and effects in prescribed burning. Restoration Ecology 3: 271-278.

Kolb, T. E., Holmberg, K. M., Wagner, M.R., and J.E. Stone. 1998. Regulation of ponderosa pine foliar physiology and insect resistance mechanisms by basal area treatments. Tree Physiology 18: 375-381.

Kozlowski, T. T. and S. G. Pallardy. 1997. Physiology of woody plants. Academic Press, San Diego, CA.

Marshall, J. D. and R. H. Waring. 1985. Predicting fine root production and turnover by monitoring root starch and soil temperature. Canadian Journal of Forest Research 15:791-800.

Martin, R.E. 1963. A basic approach to fire injury of tree stems. Tall Timbers Fire Ecology Conference Proceedings 2: 151-162. Tall Timbers Research Station, Tallahassee, FL.

McHugh, C.W. and T.E. Kolb. 2003. Ponderosa pine mortality following fire in northern Arizona. Int. J. Wildland Fire 12:1-16.

McHugh, C. W., T. E. Kolb, and J. L. Wilson. 2003. Bark beetle attacks on ponderosa pine following fire in northern Arizona. Environmental Entomology 32: 510-522.

Meldahl, R. S., N. Pederson, J. S. Kush, and J. M. Varner. 1999. Dendrochronological investigations of climate and competitive effects on longleaf pine growth. Pages 265-285 in: Tree Ring Analysis: Biological, Methodological, and Environmental Aspects. R. Wimmer and R. E. Vetter, editors. CAB International, Wallingford, UK.

Menges, E. S. and M. A. Deyrup. 2001. Postfire survival in south Florida slash pine: Interacting effects of fire intensity, fire season, vegetation, burn size, and bark beetles. International Journal of Wildland Fire 10: 53-63.

Miyanishi, K. and Johnson, E.A. 2002. Process and patterns of duff consumption in the mixedwood boreal forest. Can. J. For. Res. 32: 1285-1295.

Ostrosina, W.J., Hess, N.J., Zarnoch, S.J., Perry, T.J., and Jones, J.P. 1997. Blue-stain fungi associated with roots of southern pine trees attacked by the southern pine beetle, *Dendroctonus frontalis*. Plant Disease 81:942-945.

Ostrosina, W.J., Bannwart, D., and Roncadori, R.W. 1999. Root-infecting fungi associated with a decline of longleaf pine in the southeastern United States. Plant and Soil 27:145-150.

Ryan, K. C., D. L. Peterson, and E. D. Rheinhardt. 1988. Modeling long-term fire-caused mortality of Douglas-fir. Forest Science 34: 190-199.

Ryan, K. C. and E. D. Rheinhardt. 1988. Predicting postfire mortality of seven western conifers. Can. J. For. Res. 18: 1291-1297.

Ryan, K. C. and W. H. Frandsen. 1991. Basal injury from smoldering fires in mature *Pinus ponderosa* Laws. International Journal of Wildland Fire 1:107-118.

Ryan, K.C. 2000. Effects of fire injury on water relations of ponderosa pine. Tall Timbers Fire Ecology Conference Proceedings 21: 58-66. Tall Timbers Research Station, Tallahassee, FL.

Saveland, J.M. and L.F. Neuenschwander. 1990. A signal detection framework to evaluate models of tree mortality following fire damage. Forest Science 36:66-76.

Stephens, S.L. and M.A. Finney. 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. Forest Ecology and Management 162: 261-271.

Steward, F. R., Peter, S. and J. B. Richon. 1990. A method for predicting the depth of lethal heat penetration into mineral soil exposed to fires of various intensities. Canadian Journal of Forest Research 20: 919-926.

Swezy, D.M. and J.K. Agee. 1991. Prescribed-fire effects on fine-root and tree mortality in old-growth ponderosa pine. Canadian Journal of Forest Research 21: 626-634.

van Mantgem, P., M. Schwartz and M. Keifer. 2001. Monitoring fire effects for managed burns and wildfires: coming to terms with pseudoreplication. Natural Areas Journal 21:266-273.

van Mantgem, P. and M. Schwartz. 2004. An experimental demonstration of stem damage as a predictor of fire-caused mortality for ponderosa pine. Can. J. For. Res. 34: 1343-1347.

Varner, J.M., D.R. Gordon, F.E. Putz, and J.K. Hiers. 2005. Novel fire effects in southeastern pine forests: smoldering fire and overstory pine mortality. Restoration Ecology 13: 1-9.

Wade, D.D. and R.W. Johansen. 1987. Relating wildland fire to defoliation and mortality in pine. Pages 107-110 in Phillips, D.R. (ed.). GTR SE-42. USDA Forest Service, Southeastern Forest Experiment Station

Wade, D.D., G. Custer, J. Thorsen, P. Kaskey, J. Kush, B. Twomey, and D. Voltolina. 1997. Reintroduction of fire into fire-dependent ecosystems: Some southern examples. Tall Timbers Fire Ecology Conference Proceedings 20: 94-98. Tall Timbers Research Station, Tallahassee, FL

Wargo, P.M., Parker, J., and D.R. Houston. 1972. Starch content in roots of defoliated sugar maple. Forest Science 18: 203-204.

Wyant, J.G., P.N. Omi, and R.D. Laven. 1986. Fire-induced tree mortality in a Colorado ponderosa pine / Douglas-fir stand. Forest Science 32: 49-59.

Figures

Figure 1. The Swisher-Ordway Preserve in Putnam County, Florida, the location of experimental individual pine burning experiments.

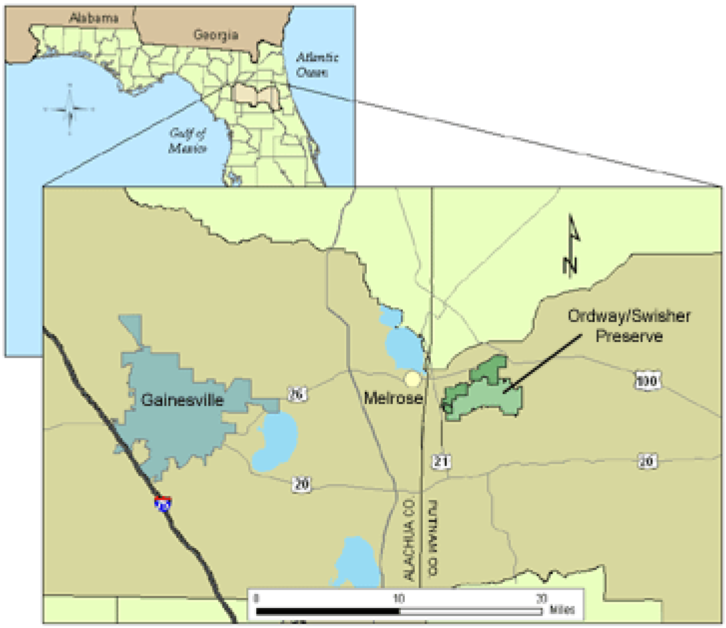


Figure 2. Experimental fire treatments subjected to individual trees in a long-unburned *Pinus palustris* forest in northern Florida, USA. The treatments were, clockwise from top right: ROOT, ROOT+STEM, STEM, and CONTROL where each treatment was designed to heat those tissues and exclude heating to other tissues (i.e., the ROOT treatment was designed to heat surface roots, and not raise the temperatures on the basal bark).

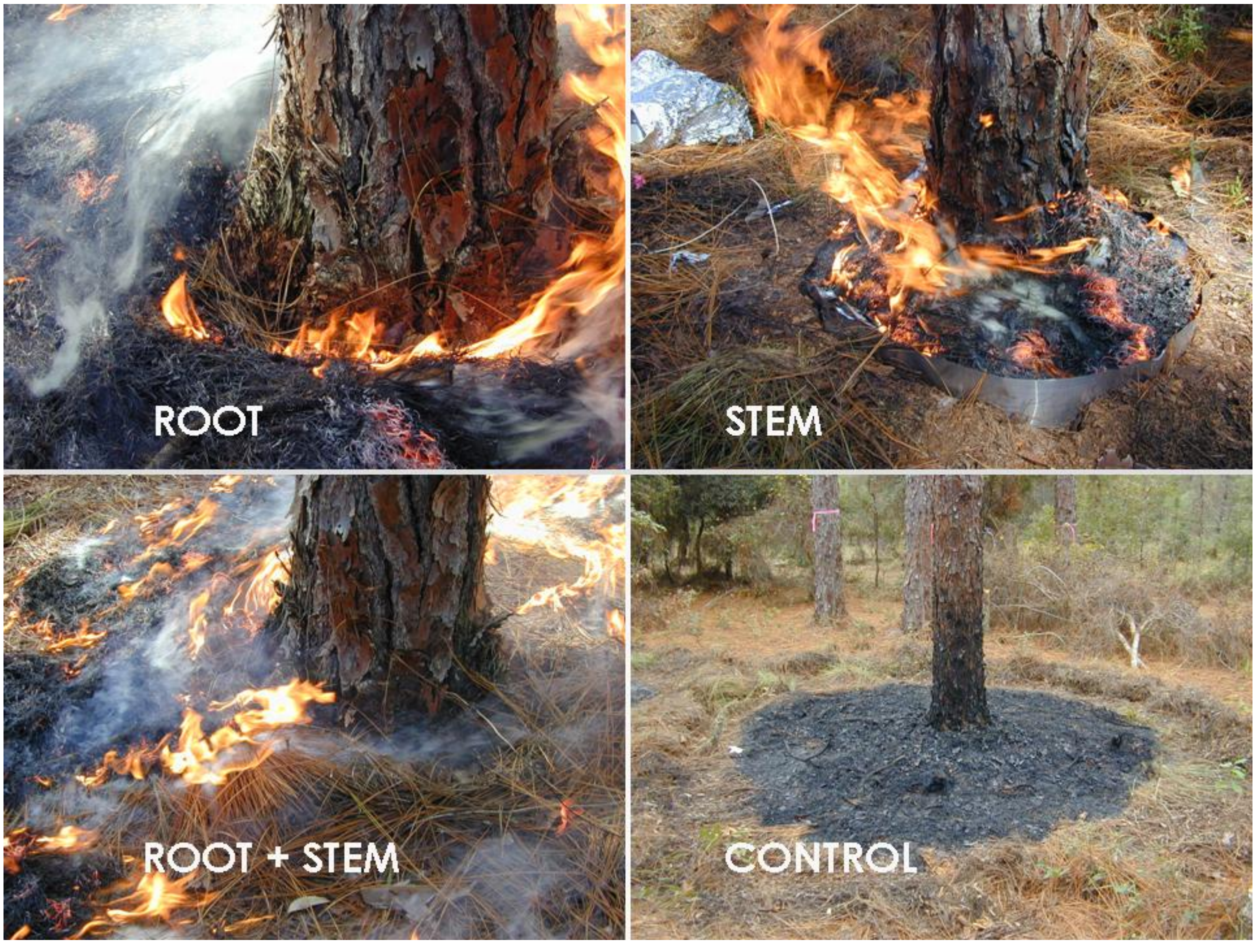
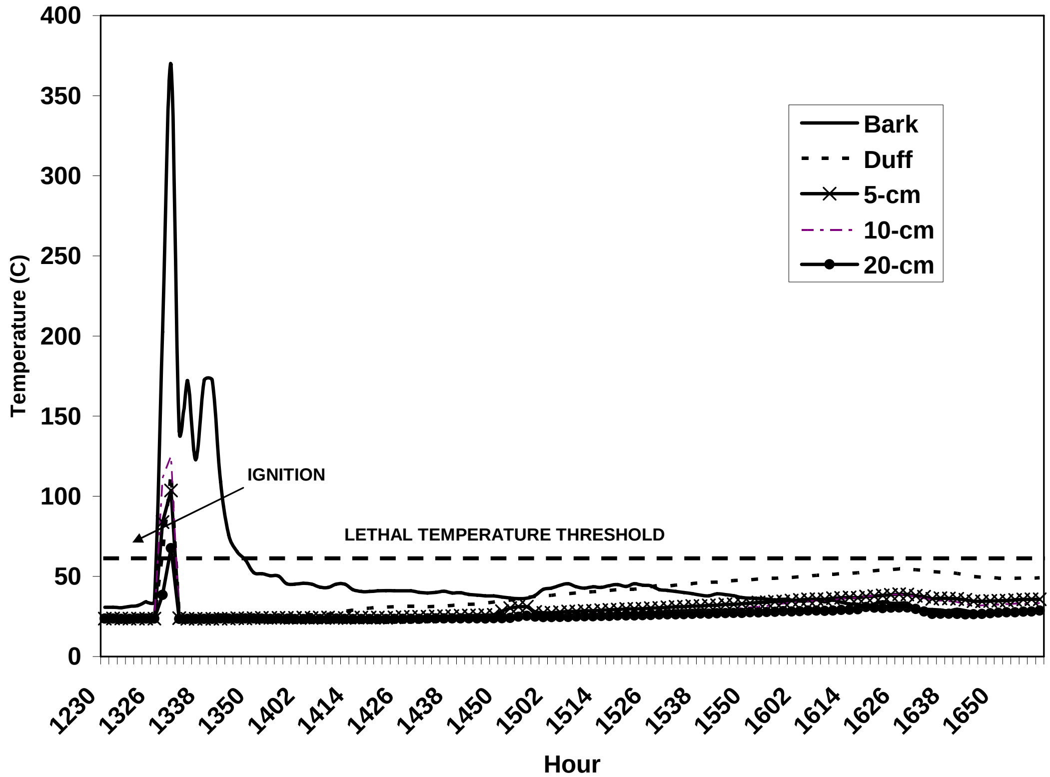


Figure 3. Mean temperatures during an experimental fire (4 November 2003- ROOT treatment) from ignition to 1700 (a) and to 0900 the following day (b).



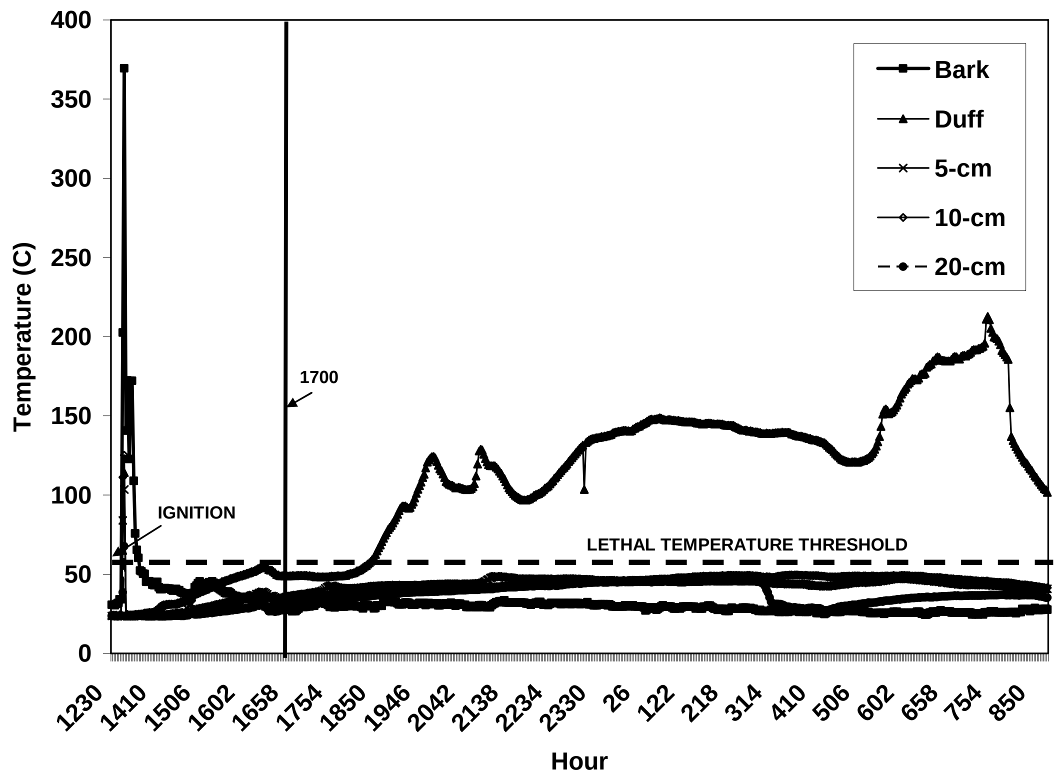


Table 1. Fire weather observations and time-of-ignition fuel moistures from experimental single-tree burns at the Swisher-Ordway Preserve, Florida, USA. All experimental fires burned between 25 September and 4 November 2003.

Weather variable	Mean ± s.d.	Max	Min
Air Temperature (ºC)	27.8 ± 2.37	32.0	25.3
Relative Humidity (%)	58.3 ± 6.19	67.0	51.0
Wind Speed (m sec^{-1})	0.9 ± 0.41	1.3	0.4
Oi moisture (%)	14.9 ± 3.4	19.1	9.4
Oe moisture (%)	64.5 ± 59.9	186.3	11.6
Oa moisture (%)	55.9 ± 23.3	100.4	36.2
Cone moisture (%)	21.0 ± 18.4	47.7	6.5
A horizon moisture (%)	7.1 ± 3.1	12.7	3.8

Table 2. Durations of lethal heating to basal bark, duff, and mineral soil during individual tree burns at the Swisher-Ordway Preserve, Florida, USA.

Treatment [a]	basal bark min > 60º C	basal duff min > 60º C	5 cm soil min > 60º C	10 cm soil min > 60º C	20 cm soil min > 60º C
STEM (n=6)	44.3 ± 77.1	42.9 ± 47.3	7.9 ± 14.1	7.3 ± 17.9	--
ROOT (n=6)	10.1 ± 7.0	145.6 ± 283.7	41.0 ± 90.5	4.6 ± 9.9	0.7 ± 0.8
ROOT + STEM (n=6)	82.2 ± 121.8	95.7 ± 187.3	56.1 ± 122.2	12.8 ± 20.9	2.1 ± 4.8
CONTROL (n=6)	9.4 ± 2.6	10.6 ± 24.6	2.7 ± 5.9	1.4 ± 3.5	0.2 ± 0.5
Means	36.5 ± 73.9	73.7 ± 168.8	26.9 ± 74.8	6.5 ± 14.4	0.8 ± 2.5

[a] Treatments were intended to isolate long-duration heating to either roots (ROOT), basal stems (STEM), both roots and stem tissues (ROOT+STEM), or no long-term smoldering (CONTROL).

Table 3. ANOVA treatment effects of individual tree fires on smoldering time, mean floor consumption, longleaf pine stem radial growth, and root nonstructural carbohydrates in northern Florida, USA.

	Burning Treatment					
	ROOT	ROOT+STEM	STEM	CONTROL	N	*P*
Smoldering time (sec)	418.9 ± 401***A***	534.5 ± 516.1***A***	410.1 ± 407.2***A***	60.9 ± 132.8 ***B***	8	0.018
Forest floor consumption (cm)	6.3 ± 1.8 ***AB***	9.1 ± 3.1***A***	7.0 ± 3.0 ***AB***	4.6 ± 2.0 ***B***	8	< 0.001
Radial growth (mm change)	-0.17 ± 0.19	-0.19 ± 0.36	-0.28 ± 0.33	-0.22 ± 0.19	8	0.582
Fine root carbohydrates (% change)	6.3 ± 16.6	12.6 ± 14.3	-9.3 ± 16.5	8.1 ± 26.3	8	0.246
Coarse root carbohydrates (% change)	-5.6 ± 27.1	-12.8 ± 46.8	-3.3 ± 44.1	9.9 ± 16.2	8	0.584

[a] Values followed by a different letter indicate significant differences among treatments, determined using a post-hoc Tukey-Kramer HSD with α= 0.05 prior to analysis.

Table 4. Step-wise multiple regression results for the analysis fuel and soil moisture effects on basal bark, duff, and mineral soil temperatures in smoldering fires in a long-unburned longleaf pine stand in northern Florida, USA.

Response variable	Equation	R^2	*P*
Basal bark temperatures > 60 C (min)	*log* (min bark > 60) = 3.86 – 0.019 (% Oa moisture)^2 0.16	0.053	
Duff temperatures > 60 C (min)	*log* (min duff > 60) = 3.61 – 0.018 (% Oe moisture)^2 0.24	0.015	
5-cm mineral soil temperatures > 60 C (min)	n/a		NS
10-cm mineral soil temperatures > 60 C (min)	n/a		NS
20-cm mineral soil temperatures > 60 C (min)	n/a		NS

Table 5. Effects of basal bark, duff, and mineral soil temperatures on longleaf pine stem radial growth and root nonstructural carbohydrates following in individual tree fires in northern Florida, USA. Results are based on step-wise linear regressions with minuets of basal heating > 60° C, duff heating > 60°, 5-cm mineral soil > 60°, 10-cm mineral soil > 60°, and 20-cm mineral soil > 60° as potential predictor variables.

Response variable	β_0	β_1	R^2	*P*
Radial growth (% change 2003-2004)	growth (mm) = -0.22	+ 0.045 *log* (5-cm min > 60)	0.16	0.080
Earlywood growth (% change 2003-2004)		n/a		NS
Latewood growth (% change 2003-2004)	lw growth (mm) = 21.7	- 19.4 *log* (10-cm min > 60)	0.17	0.069
Fine root carbohydrates (% change 2003-2004)		n/a		NS
Coarse root carbohydrates coarse (% change 2003-2004)	(% change) = 8.44	- 37.44 *log* (5-cm min > 60)	0.59	0.009

APPENDIX G.

Northwest Science 78:322-333

Burning Characteristics of Cones from Eight Pine Species

R. W. Fonda[1], Biology Department, Western Washington University, Bellingham, Washington 98225-9160, and **J.** M. Varner[2], School of Natural Resources and Environment, University of Florida, Gainesville, Florida 32611-8526

[1] Author to whom correspondence should be addressed. Current address: 1646 Sudden Valley, Bellingham, WA, 98229. E-mail:richfonda@comcast.net
[2] Current address: Department of Forestry and Watershed Management, Humboldt State University, Arcata, CA, 95521

Abstract
This experiment studied burning characteristics of pine cones as a separate fuel component. Cones of fire resisters ponderosa pine, Jeffrey pine, longleaf pine, and south Florida slash pine, and cones of fire evaders Monterey pine, knobcone pine, sand pine, and pond pine were burned in a fire chamber. The experiment tested fire adaptive strategy (resisters vs. evaders), geographic region (western vs. eastern U.S.A.), and interactions between those two factors in a 2x2 factorial experiment. Jeffrey pine, longleaf pine, and south Florida slash pine supported the longest flames, smolder times, and burn times; they also lost >89% of cone mass. Monterey pine and knobcone pine sustained flames that lasted >10 min. Cones of Monterey pine, sand pine, and pond pine lost <50% cone mass. Resisters significantly exceeded evaders in all burning categories except flame time and mean rate of weight loss. Western pines significantly exceeded eastern pines in all burning categories except flame length and percent fuel combusted. Significant interactions between fire adaptive strategy and geographic region existed for all burning characteristics except mean rate of weight loss. The interaction was accounted for by cones of eastern evaders, which had the lowest mean values for most characteristics. Only recently have cones been regarded as a separate fuel component, yet they contribute more to fire regimes in their communities than previously thought. Fire models might be more accurate if they incorporate the contributions of cones to fire regimes. Furthermore, smoke emitted by smoldering cones is an important smoke management concern.

Introduction
The typical pine life cycle described in botany textbooks depicts cones opening and releasing seeds in the second growing season after cones are formed. Species with serotinous cones, however, are an exception. These cones commonly remain closed on the tree, impregnated with resin and sealed shut until heat from a stand-replacing fire opens them. The seeds are released to germinate on the postfire landscape, forming the next forest.

Depending on which strategy they use to adapt to repeated fires in their environment, pines are classified into two groups. Species that use a strategy of cone serotiny are evaders (Rowe 1983, Agee 1993, Fonda et al. 1998, Fonda 2001), and forests they dominate are termed fire-resilient (Fonda et al. 1998, Fonda 2001). These forests typically support high intensity crown fires and occasional surface fires, in which the entire stand is killed (Abrahamson 1984, Myers 1985, Vogl et al. 1988, Harms 1996, Schwilk and Ackerly 2001). Continued dominance of pines depends heavily on the success of seed in the serotinous (closed) cones. Except for a few species that resprout, such as pond pine (*Pinus serotina*) (Fowells 1965), most parent trees do not survive the fire. The importance of cone serotiny as an evolutionary strategy for fire evaders is demonstrated by the significant negative correlation that exists between cone serotiny and self-pruning, leaf length, needle density, twig thickness, and minimum reproductive age (Schwilk and Ackerly 2001). Cone serotiny represents a co-evolution strategy with traits that typify fire evaders (Schwilk and Ackerly 2001). Because evaders maintain cones in the canopy for many years, only occasionally dropping them, litter layers in fire-resilient forests are sparsely populated with fallen cones (Figure 1). Often these cones are attached to twigs that have broken from parent trees.

The other group of pines comprises species that have developed different strategies to resist and survive fire, and their cones have few to no fire adaptive values (Schwilk and Ackerly 2001). In this article, we will refer to these pine cones with reflexed cone scales as open cones, to contrast with closed serotinous cones. Species for which cones are fire-neutral are resisters (Rowe 1983, Agee 1993, Fonda et al. 1998, Fonda 2001), and forests they dominate are termed fire-stable (Fonda et al. 1998, Fonda 2001). Typically, fire-stable forests support low intensity surface fires in highly flammable fine fuels (Sweeney 1967, Vogl 1967, Williamson and Black 1981, Arno and Peterson 1983, van Wagtendonk 1983, Myers 1985, Agee 1994). Continued survival of resister species depends on thick bark, fire-resistant bark, self-pruning, or thick needle clusters that protect meristems and aerial portions of the trees. Because resisters shed cones frequently, litter layers in fire-stable forests are heavily populated with downed cones (Figure 2).

Reviews of wildland fire ecology focus on fire regimes, behavior, severity, effects, history, and management (Agee 1993, Pyne et al. 1996). These books, which summarize the existing body of fire ecology knowledge, contain no references to cones as a fuel source. The fuel model is one of the main components of any fire behavior model, and several fuel model descriptions and classifications exist (Rothermel 1972, Albini 1976, Anderson 1982, Andrews and Chase 1989, Andrews and Bradshaw 1997). None of these identifies cones as a separate fuel component. Perhaps those who should be most aware of cones as a fuel source are involved with fire suppression, however, a typical publication for wildland firefighters (Teie 1994) has no text on how cones relate to fire suppression efforts. Cones are essentially the invisible fuel.

Cone fuels have been considered in fire science, albeit predominantly in passing. Brown et al. (1982) include cones in the litter layer for purposes of calculating fuel loadings. Cones, however, were not specifically isolated as a separate fuel component, and in the example given in Brown et al. (1982) the contribution of cones to the 0.09 kg m^{-2} fuel loading in the litter layer of a lodgepole pine (*P. contorta*) forest is not identified. Clements (1976) investigated firebrands (long-distance embers that cause spot fires) for fuels in the eastern United States. He studied cones of six pine species, including longleaf (*P. palustris*), slash (*P. elliottii*), and pond pine, measuring their terminal velocity and burn out times. He concluded that cones represented significant firebrand fuels, but placed no more emphasis on cones than any of the other 25 firebrand fuels (Clements 1976).

In a study of 19 Sierra Nevada conifers van Wagtendonk et al. (1998) identified cones as a fuel component separate from the common categories used in most fire behavior models. Mean heat contents of the 19 species varied narrowly from 21.22 MJ kg^{-1} with ash to 21.64 MJ kg^{-1} without ash, but differences among species were not significant. Because these heat contents were not substantially different from heat contents calculated for foliage, duff, and woody fuels, contributions of cones to fireline intensity should be considered in fuel calculations for wildland fires. The values for Sierra Nevada fuel components were higher than standard values used in fuel models to predict fire behavior, which could predict lower fireline intensities than actually encountered. Cone fuels contributed to these overall values. To our knowledge, van Wagtendonk et al. (1998) is the only reference that recognizes cones as a separate fuel component.

The burning characteristics of needles from eight species of pines were investigated recently to examine aspects of flammability, and to compare fire resisters with fire evaders and western pines with eastern pines (Fonda 2001). Differences existed among the eight species, between resisters and evaders, and between western and eastern pines. Significant interactions existed between fire adaptive strategy and geographic region for all burning characteristics except mean rate of weight loss. The interaction was accounted for primarily by differences between western evaders, which had high values for most burning characteristics, and eastern evaders, which had some of the lowest values. In this study, we examined pond pine and all but jack pine (*P. banksiana*) of the eight species studied by

Fonda et al. (2001) to determine how their cones contribute to the same aspects of flammability examined previously for pine needles.

The eight pines studied here (Table 1) were an ideal group to investigate the relationship between flammability of cones and fire adaptive strategies in fire-stable and fire-resilient communities. The research was designed to compare 1) differences among the eight pine species, 2) four resisters with four evaders, 3) four western pines with four eastern pines, 4) two western resisters with two eastern resisters, 5) and two western evaders with two eastern evaders, and to analyze the interaction between fire adaptive strategy and geographic region.

Methods

Experimental Design

We used the same basic method described in Fonda et al. (1998) and Fonda (2001), burning 10 cones of each species for a total of 80 burns. The research was a 2x2 factorial experiment in a completely randomized design (CRD) ANOVA, with the significance level set at P=0.05 before the research began. This design allowed us to designate species as a treatment effect, and to test for significant differences according to a basic CRD analysis. The two main factors (A: fire adaptive strategy and B: geographic region) combined to contribute four treatments: western resisters, eastern resisters, western evaders, and eastern evaders. These combinations, the main factors, and the interactions between the main factors were tested for significant differences for each burning characteristic by standard factorial analysis (Zar 1999). Significant differences among more than two treatments for each burning characteristic were judged by a Newman-Keuls multiple range test (MRT). Data for percent fuel combustion were transformed by arcsin before analysis.

Field Collections

Cones from the litter layer were collected in August-October 2002 at several locations from sites on which only the targeted pine species grew (Table 1). Only cones that fell before summer 2002, and that showed no signs of decomposition, were collected. At least 15 cones were collected from each location and taken to Western Washington University, from which 10 were randomly chosen to be burned. We did not knowingly collect more than one pine cone from a given parent tree. The cones of each species were allowed to air dry, then oven dried for at least 72 hr at 100^{o}C. Cones were removed from the oven, allowed ~20 min for weight to stabilize, then weighed. Mean fuel moisture at the time of burning ranged from 0.3% (Monterey pine) to 2.3% (ponderosa pine). Equilibrium fuel moisture during fire weather is on the order of 1-3% (Agee 1993), and we elected to burn all cones at approximately those values.

Burning Characteristics

We used a fire chamber to study burning characteristics of cones from these eight pine species (Figure 3) as indicators of flammability for this fuel component. Flammability has four components: ignitability, combustibility (intensity) and consummability of the fuel, and sustainability of the fire (Martin et al. 1994). This work relates to intensity (flame length), sustainability (flame time, smolder time, and burn time), and consummability (percent fuel combustion and mean rate of weight loss), as defined by Fonda et al. (1998) and Fonda (2001).

The fire chamber was 1 m^2 x 3 m tall, with a four-story exhaust chimney. Excessive draw from the chimney over the fire bed was prevented by a series of baffles in the chimney, and air movement was controlled by a fan in the chimney. Mean air velocity over the fuel bed was 9.9 cm sec^{-1} (Fonda et al. 1998, Fonda 2001).

Each cone was placed on the floor of the fire chamber on three 15-cm xylene-soaked strings. Strings were ignited, and two timers were started when fuels first ignited. Maximum flame length was compared against a 2-m rule on the rear wall of the fire chamber. This 5-cm wide steel rule, with prominent 1-cm markings, was machined specifically for this fire chamber. Distance between the flames and the steel rule was ~30 cm. After flame length was recorded, room lights were turned off for judging flame and burn times. We used a mirror to observe flames, embers, and smoke on the back side of the cones.

The first timer was stopped when all flames were extinguished, the second when the last ember was extinguished or when smoke no longer was emitted, whichever came last. The first timer measured flame time, the second measured burn time, and the difference between the two was smolder (ember) time. For cones of sand pine and pond pine, which smoked during the smoldering period, we used a flashlight beam to highlight the smoke against the mirror. In cases for which we were unsure if smoke was no longer being emitted, a third timer was started at the time we suspected smoldering had ended while we continued to watch the cone for at least 60 sec to be certain. This extra time was subtracted from the second timer once we stopped the two timers.

Unburned string was removed, and unconsumed ashes were weighed. Percent fuel combusted was calculated by dividing consumed weight by initial weight. Mean rate of weight loss was calculated as mg lost over burn time.

Because cone weights varied widely across the eight species, all data were analyzed to identify burning characteristics that correlated significantly with cone weight.

In nature, cones are embedded in the needle layer on a forest floor. We wanted to know how burning characteristics would differ if the cones were ignited by the needle litter, rather than by string. Means SE were calculated for cone weights for each species, based on the 80 cones we burned individually. One unburned cone of each species within 2 SE of the mean (i.e., not significantly different from the mean weight) was selected to be burned on 15 g of ponderosa pine needles (i.e., the fuel source was constant). These cones and needles were oven-dried at 100°C for 72 hr, then burned according to the same protocol as previously. Values for each burning characteristic for the cones burned with needles were compared to mean values of the same burning characteristics derived from individual cones in a paired t-test, wherein each species was a pairing factor.

Results

Burning Behavior

Among the resisters, longleaf pine and Jeffrey pine cones burned nearly completely to white ash. The cones glowed red as soon as flames began, and white ash appeared well before flames were extinguished. Longleaf pine was the only species for which we heard an audible whooshing sound as the cones caught fire. South Florida slash pine cones also glowed red with flames, and emitted dense smoke when flames were extinguished. These cones burned nearly as completely as Jeffrey pine and longleaf pine, but some blackened cone scales remained. Ponderosa pine cones never created white ash; all ended the burn period with heavily blackened cones.

Serotinous cones burned incompletely, and finished the burn period with heavily charred cone scales. All closed cones in this study had dense whorls of thick cone scales at their bases (Figure 3). All four species emitted flames from the basal whorl, but none of the scales was consumed. Only the distal, slightly open, scales glowed red and were consumed by flames and smoldering. Knobcone and Monterey pine cones smoldered with abundant embers and little smoke, in contrast to sand and pond pine cones for which flames and embers were extinguished simultaneously. The smolder times for these cones were judged by smoke emissions.

Burning Characteristics of Individual Species

Mean maximum flame length was significantly greater for longleaf pine than all other species, and all test burns exceeded 80 cm. Jeffrey pine had significantly longer mean maximum flame lengths than the other six species (Table 2), but only one cone supported flames as long as 80 cm. Mean maximum flame length did not differ significantly between south Florida slash pine and ponderosa pine, between Monterey pine and knobcone pine, and between sand pine and pond pine. Sand pine and pond pine had the shortest flames.

Mean flame times for Monterey pine and knobcone pine were not significantly different, and both species flamed significantly longer than all other species (Table 2). There were no significant differences among the remaining six species. Maximum/minimum flame times were 1094/533 sec for knobcone pine and 935/339 sec for Monterey pine. The next two longest flame times among the other six species were 910 and 504 sec (Jeffrey pine). Every species had at least one cone that flamed for 300 sec, and 40 of the 80 burned cones flamed for 300 sec.

Smolder times are the noteworthy burning characteristic for these pine species. Jeffrey pine cones smoldered significantly longer than all other species (Table 2). Four Jeffrey pine cones smoldered for >5000 sec. Longleaf pine and south Florida slash pine did not differ significantly, nor did Monterey pine, knobcone pine, and ponderosa pine. Of the 20 cones burned for longleaf pine and south Florida slash pine, 11 smoldered for longer than 2500 sec. Of the 30 cones burned for Monterey, knobcone, and ponderosa pine, three exceeded 2500 sec. Pond pine and sand pine were not significantly different, and had the shortest smolder times of the eight species.

Mean burn times followed the same order as smolder times, although more differences were significant for this burning characteristic (Table 2). Jeffrey pine and longleaf pine ranked first and second, and both were significantly longer than the other species. Two Jeffrey pine cones had total burn times >6000 sec. Maximum burn time for longleaf pine was 3755 sec. Differences among south Florida slash pine, Monterey pine, and knobcone pine were not significant. As with smolder time, sand pine and pond pine were not significantly different, and had significantly shorter burn times than the other species. Maximum burn times for these species were <650 sec.

Mean percent fuel combusted did not differ significantly among longleaf pine, Jeffrey pine, and south Florida slash pine, for which at least 88% of the fuel was consumed. (Table 2). These species were significantly greater than any others. Ponderosa pine cones lost nearly 80% of their mass. Knobcone pine had the highest percent combustion of the closed cone pines, but significantly lower than ponderosa pine. Percent combustion among sand pine, Monterey pine, and pond pine did not differ significantly; all were <50% combusted.

Mean rate of weight loss provides little information on which to separate the species (Table 2). South Florida slash pine had a significantly lower rate than other species, and sand pine was next lowest. The others were mostly not significantly different, and the overlap between knobcone pine and ponderosa pine indicates that a gradient of rates existed among these cones. All lost weight at values between 17 and 29 mg sec^{-1}.

Mean cone weights for Jeffrey pine and Monterey pine were not significantly different from each other, and they were significantly heavier than the other species (Table 2). Knobcone pine and longleaf pine were each significantly different from all others, and significantly heavier than the remaining four species. Mean weights of these above four species all exceeded 50 g. Mean weights of the remaining four species were <25 g. Ponderosa pine, south Florida slash pine, and pond pine did not differ significantly. Sand pine had significantly lighter cones than any other species. Cone weights correlated significantly with three burning characteristics. Heavier cones had longer flame lengths, smolder times, and burn times. No other characteristics correlated significantly with cone weights.

Values in Table 2 are based on individual cones burning on the floor of the burn chamber. For cones burned with pine needles as the ignition source, smolder times were significantly longer by 1302 sec, burn times were significantly longer by 1338 sec, and percent combusted was significantly greater by 8.3%. Mean rate of weight loss was significantly lower by 9.3 mg sec^{-1}. The most important effect for cones burned with pine needles was longer smolder times, which led to longer burn times and greater fuel consumption. The greater heat created by the pine needle bed involved more of the core of the cone in combustion.

Treatments Combining Fire Adaptive Strategy and Geographic Region

Flame length is a measure of fire intensity. Eastern resisters had significantly longer flames than all other combinations, followed by western resisters (Table 3); both groups exceeded 60 cm. Flame lengths for western evaders and eastern evaders were not significantly different; both groups were <50 cm.

For measures of fire sustainability (flame, smolder, and total burn time), western evaders supported significantly longer flame times than all other combinations, among which there were no significant differences (Table 3). Western resisters and eastern resisters had significantly longer smolder times and burn times than other groups. Eastern evaders had the shortest smolder and burn times (Table 3). Western evaders were significantly longer, by a considerable difference, in both categories than eastern evaders.

For measures of consummability, percent fuel combusted differed significantly among all groups (Table 3). Western resisters lost over 90% of cone mass, followed by eastern resisters. Western evaders lost >50% of cone mass, whereas eastern evaders lost <50% of cone mass. Mean rate of weight loss did not differ significantly between western resisters and western evaders, nor between eastern resisters and eastern evaders (Table 3). Western resisters and western evaders had significantly higher rates of weight loss than eastern resisters and eastern evaders.

Mean cone weights differed significantly across all groups (Table 3). Western evaders had the heaviest cones, followed by western resisters and eastern resisters. The lightest cones in the experiment were eastern evaders.

Main Effects of Fire Adaptive Strategy and Geographic Region

For the main effects of fire adaptive strategy, resisters had significantly greater flame lengths, smolder time, burn time, and percent fuel combusted (Table 4). Evaders had significantly longer flame times. The differences between resisters and evaders for mean rate of weight loss and cone weight were not significant. Of the top four species for flame length, smolder time, burn time, and percent fuel combusted at least three were resisters, whereas the three top species f or flame time were evaders (Table 2). Except for flame time, resisters had higher values for characteristics relating to intensity, sustainability, and consummability.

For the main effects of geographic region, western species had significantly larger values for flame time, smolder time, burn time, mean rate of weight loss, and cone weight (Table 5). The differences between western and eastern pines for maximum flame length and percent fuel combusted were not significant. Western species had significantly higher values for all characteristics relating to intensity, sustainability, and consummability.

Factor Interaction

Significant interactions between fire adaptive strategy and geographic region existed for all burning characteristics except mean rate of weight loss (Figure 4). The midpoints on the lines connecting the W,R-E,R and W,E-E,E pairs represent the central tendencies of the groups, and the vertical difference between the two midpoints identifies the magnitude of the interaction. For instance, the midpoints for weight loss are extremely close, thus the interaction of 0.66 is not significant. Conversely, the midpoints for all other burn characteristics are widely separated and significant. The main effects of the factors for each burning characteristic (Tables 4, 5) were affected significantly by the interactions, which are reciprocal within the burning categories. Strategy contributed strongly to every interaction except cone weight. Region contributed strongly to cone weight, flame, smolder, and burn times, but contributed only slightly to the interactions involving flame lengths and percent fuel combusted. In general, interactions were driven by responses from eastern evaders, which had the lowest mean values for most characteristics (Figure 4). Only for flame time were western evaders the top-ranked group.

Discussion

The data from this study exemplify differences in cones relative to fire adaptive strategies. Resisters burned for a long time and to white ash, with high values for percent fuel consumption (Table 4). Evaders (particularly Monterey pine and knobcone pine) supported flames for significantly longer times than resisters, but otherwise resisters had higher values in all burn categories. The constant characteristic among the evaders was the low percentage of cone mass combusted by fire (Tables 2-4). Differences between open and closed cones drove the significant interactions in this study. Regional differences centered on the timed characteristics, for which the western species had significantly higher values (Table 5). Flame lengths and percent fuel combusted did not differ significantly between eastern and western species. Cone serotiny is negatively correlated with several traits associated with fire in pines (Schwilk and Ackerly 2001). The long flame times of knobcone pine and Monterey pine for the cones (Table 2) and needles (Fonda et al. 1998, Fonda 2001) are strategies that should enable crown fires. Forests dominated by these species typically have abundant ladder fuels when they are fire-prone, so that flames from the cones and needles should ignite the ladder fuels, leading to a crown fire. The cones and needles of sand pine and pond pine (Figure 1), however, are less likely to ignite ladder fuels.

These eight pines are prominent in communities for which fire is an important environmental factor, and virtually all authors of papers exploring fire relationships mention their highly flammable fine fuels. We compared mean values for each burning characteristic for cones (Table 2) against needles (Fonda 2001; Table 6) by paired t-tests. Cones had significantly longer flame, smolder, and burn times, whereas needles had significantly greater flame length, percent combusted, and rates of weight loss. It is also noteworthy that flame times of cones (Table 2) were not significantly different from total burn times of needles (Fonda 2001). Cones are clearly an important fuel component in pine forest fire regimes, especially when combined with needles. These two components should ensure fire sustainability and consummability in ecosystems dominated by resisters, and they should help pre-heat and ignite ladder fuels in forests dominated by western evaders.

Smoke production has become an important consideration in wildland fire. The data for these cones (Tables 2-5) indicate that burning and smoldering cones contribute to the smoke environment for time periods that cannot be ignored. Except for eastern evaders, the other groups produced smoke for well over 30 min (Table 3). Jeffrey pine averaged > 1 hr of smoke production (Table 2).

Regardless of geographic location, all four resisters dominate communities in which surface fires are common, and their burning characteristics demonstrate that they produce highly flammable cones (Table 2). Jeffrey pine and ponderosa pine had the most flammable needles of 13 western conifers (Fonda et al. 1998). Longleaf pine and south Florida slash pine had some of the longest flames from needles (Fonda 2001). The cones of these four species clearly augment the surface fire regime created by the needles (Figure 2), yet their role has been unrecognized. Surface fires that might be carried poorly by minimal fine fuel loads should move more dependably when cones fill in gaps in the fuel bed and are an additional flame source. Cone fuels may also maintain competition-free environments surrounding resister pines in a kill thy neighbor strategy (*sensu* Bond and Midgley 1995). Taylor and Fonda (1990) noted that fuels in a ponderosa pine stand were not concentrated near trees, ignoring the clustered cones that are so common in these stands. Ponderosa pine and Jeffrey pine cones had longer flame, smolder, and burn times than needles, although cones had shorter flame lengths. Rather than being fire-neutral, these pines have invested the same kind of highly flammable strategies in cones that they invested in needles.

Western evaders dominate forests in which surface and crown fires are common. Their needles are highly flammable, with long flames, long flame times, and the longest burning times (Fonda et al. 1998, Fonda 2001). Their cones contribute to the fuel layer, although they are less concentrated on the forest floor than cones from resisters. The heavy cones of Monterey pine and knobcone pine supported flames for >10 min (Table 2), and they had longer burn times than the eastern evaders (Table 3). The combination of high needle flammability and long flame and ember times of cones ensures that surface fuels ignite ladder fuels and initiate the crown fires on which seed release depends. Abundant cones in the canopies should help sustain fire in the crowns, as suggested by Clements (1976). Even with these high values for flammability, it is significant that cones were only ~50% combusted (Tables 2, 3). The strategy to protect seeds against fire by developing cones that resist consumption is paramount with these evaders.

In contrast to western evaders, forests dominated by eastern evaders generally do not support surface fires (Myers 1985). Crown fires are characteristic of fires in sand pine (Myers 1990), less so in pond pine communities (Harms 1996). Jack pine needles were burned by Fonda (2001), and they proved to be among the least flammable pine needles. Because we used pond pine cones in this test, we wanted to know how needle flammability differed between these two species, which would provide more information on how cones and needles relate to fire behavior in forests dominated by eastern evaders. Ten 15-g samples of pond pine needles were burned according to the above protocol and compared to jack pine data (Fonda 2001). Pond pine needles were more flammable than jack pine and sand pine, except that pond pine flame times were significantly shorter (Table 6). Pond pine needles produced flames that were significantly longer than any pine species tested previously (Fonda et al. 1998, Fonda 2001), which might be a factor in initiating surface fires in the dense pond pine understory. Although the short burn times for pond pine and sand pine did not differ significantly for either needles or cones (Tables 2, 6), sand pine needles had longer flame times whereas pond pine needles had longer ember times. As with western evaders, fuel consumption was low for eastern evader cones (Tables 2, 3). Perhaps most importantly, these cones smoldered with no glowing embers, and total burn time was ~450 sec (Table 3). All of these data argue that needles and cones are unlikely to contribute sufficient fire to ignite a crown fire in eastern evader communities, especially compared to western evader communities.

Only recently have cones been regarded as a separate and distinct fuel component (van Wagtendonk et al. 1998). Heat contents of foliage, duff, woody fuels, and cones of Sierra Nevada conifers were about equal, but they were higher than standard values commonly used in fuel models (van Wagtendonk et al. 1998). Although they did not study cones, Williamson and Agee (2002) demonstrated that foliar heat contents of three interior Pacific Northwest conifers also were higher than standard values. These authors demonstrated that models that ignored the different heat contents of these fuel components were liable to underestimate fireline intensity, and van Wagtendonk et al. (1998) further implied that ignoring cones would result in miscalculations. Indeed, heat content with ash varied narrowly among knobcone pine, Jeffrey pine, and ponderosa pine cones in the Sierra Nevada (20.73-22.52 MJ kg^{-1}), yet the cones of each species burned quite differently (Table 2).

Fire behavior models should incorporate the diversity in flammability of fuels with similar shapes, sizes, and heat contents (i.e., their burning characteristics), and also their placement in the fuel bed. The burning characteristics of these eight pine species (Tables 2-5) indicate that they contribute more to fire regimes of their communities than previously thought. Closed cones and open cones respond differently to fire, as do western and eastern species. Models for forests in which the dominant species are resisters, whether east or west, should account for the burn times of the cones (Tables 2, 3) and their ability to ignite fine fuels to sustain surface fires. Furthermore, because cones in resister-dominated forests invariably are distributed evenly throughout the fuel layer, they sustain surface fires and serve as vectors of ground fires when they are abundant.

Models for evader-dominated forests should differ according to eastern and western species. The large cones of western evaders supported flames for a mean of >11 min (Table 3). Although these cones are scarcer in the fuel layer compared to resisters, they still are capable of igniting abundant fine fuels that characterize mature western evader-dominated forests. These cones are also likely to ignite in the tree canopies, further enhancing the likelihood of a crown fire. On the other hand, our data argue that models for eastern evader-dominated forests would not benefit from recognizing cones as a significant contributor to the fire environment. All of their burning characteristics are unimportant in starting or carrying ground fires.

Although differences in the importance of cone fuels exist among fire-adaptive strategies (i.e., cone serotiny) and geographic region, it is evident that future models should better incorporate these factors and begin to recognize the role of cones, heretofore an invisible wildland fuel.

Acknowledgements

We are pleased to thank Sara Pattinson, Thomas Jentz, Gweneth and Larry Bliss, and Ken Gray for help with cone collection. Jeannie Gilbert created Figure 4. David Peterson and Jan van Wagtendonk provided excellent, constructive reviews for which we are grateful. This research was partially supported by the Bureau for Faculty Research, Western Washington University, and the USDI/USDA Joint Fire Science Program.

Literature Cited

Abrahamson, W. G. 1984. Species responses to fire on the Florida Lake Wales Ridge. American Journal of Botany 71:35-43.

Agee, J. K. 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Covelo, California.

Agee, J. K. 1994. Fire and weather disturbances in terrestrial ecosystems of the eastern Cascades. USDA Forest Service General Technical Report PNW-GTR-320. Pacific Northwest Research Station, Portland, Oregon.

Albini, F. A. 1976. Estimating wildfire behavior and effects. USDA Forest Service General Technical Report INT-30. Intermountain Research Station, Ogden, Utah.

Anderson, H. E. 1982. Aids to determining fuel models for estimating fire behavior. USDA Forest Service General Technical Report INT-122. Intermountain Research Station, Ogden, Utah.

Andrews, P. L., and L. S. Bradshaw. 1997. FIRES: Fire information and retrieval and evaluation system – a program for fire danger rating analysis. USDA Forest Service General Technical Report INT-GTR-367. Intermountain Research Station, Ogden, Utah.

Andrews, P. L., and C. H. Chase. 1989. BEHAVE: Fire behavior prediction and fuel modeling system – BURN subsystem, part 2. USDA Forest Service General Technical Report INT-260. Intermountain Research Station, Ogden, Utah.

Arno, S. F., and T. D. Peterson. 1983. Variation in estimates of fire intervals: a closer look at fire history on the Bitterroot National Forest. USDA Forest Service Research Paper INT-301. Intermountain Research Station, Ogden, Utah.

Bond, W. J., and J. J. Midgley. 1995. Kill thy neighbour: an individualistic argument for the evolution of flammability. Oikos 73:79-85.

Brown, J. K., R. D. Oberheu, and C. M. Johnston. 1982. Handbook for inventorying surface fuels and biomass in the interior West. USDA Forest Service General Technical Report INT-129. Intermountain Research Station, Ogden, Utah.

Clements, H. B. 1976. Lift-off of forest firebrands. USDA Forest Service Research Paper SE-159. Southeastern Forest Experiment Station, Asheville, North Carolina.

Fonda, R. W., L. A. Belanger, and L. L. Burley. 1998. Burning characteristics of western conifer needles. Northwest Science 72:1-9.

Fonda, R. W. 2001. Burning characteristics of needles from eight pine species. Forest Science 47:390-396.

Fowells, H. A. (technical coordinator). 1965. Silvics of Forest Trees of the United States. USDA Forest Service Agricultural Handbook No. 271. U.S. Government Printing Office, Washington, D.C.

Harms, W. R. 1996. An old-growth definition for wet pine forests, woodlands, and savannas. USDA Forest Service General Technical Report SRS-2. Southern Research Station, Asheville, North Carolina.

Martin, R. E., D. A. Gordon, M. E. Gutierrez, D. S. Lee, D. M. Molina, R. A. Schroeder, D. B. Sapsis, S. L. Stephens, and M. Chambers. 1994. Assessing the flammability of domestic and wildland vegetation. Pages 130-137 *In* Proceedings of the 12th Conference on Fire and Forest Meteorology. Society of American Foresters, Bethesda, Maryland.

Myers, R. L. 1985. Fire and the dynamic relationship between Florida sandhill and sand pine scrub vegetation. Bulletin of the Torrey Botanical Club 112:241-252.

Myers, R. L. 1990. Scrub and high pine. Pages 150-193 *In* R. L. Myers and J. J. Ewel (editors), Ecosystems of Florida. University of Florida Press, Gainesville, Florida.

Pyne, S. J., P. L. Andrews, and R. D. Laven. 1996. Introduction to Wildland Fire. Wiley, New York.

Rothermel, R. C. 1972. A mathematical model for predicting fire spread in wildland fuels. USDA Forest Service Research Paper INT-115. Intermountain Research Station, Ogden, Utah.

Rowe, J. S. 1983. Concepts of fire effects on plant individuals and species. Pages 135-154 *In* R. W. Wein and D. A. MacLean (editors), The Role of Fire in Northern Circumpolar Ecosystems. Wiley, New York.

Schwilk, D. W., and D. D. Ackerly. 2001. Flammability and serotiny as strategies: correlated evolution in pines. Oikos 94:326-336.

Sweeney, J. R. 1967. Ecology of some fire type vegetation in northern California. Proceedings of the Tall Timbers Fire Ecology Conference 7:111-125.

Taylor, K. L., and R. W. Fonda. 1990. Woody fuel structure and fire in subalpine fir forests, Olympic National Park, Washington. Canadian Journal of Forest Research 20:193-199.

Teie, W. C. 1994. Firefighter's Handbook on Wildland Firefighting. Strategy, Tactics and Safety. Deer Valley Press, Rescue, California.

van Wagtendonk, J. W.1983. Fire suppression effects on fuels and succession in short-fire-interval wilderness ecosystems. Pages 119-129 *In* J. E. Lotan, B. M. Kilgore, W. C. Fischer, and R. W. Mutch (technical coordinators), Proceedings of a Symposium and Workshop on Wilderness Fire. USDA Forest Service General Technical Report INT-182. Intermountain Research Station, Ogden, Utah.

van Wagtendonk, J. W., W. M. Sydoriak, and J. M. Benedict. 1998. Heat content variation in Sierra Nevada conifers. International Journal of Wildland Fire 8:147-158.

Vogl, R. J. 1967. Fire adaptations of some southern California plants. Proceedings of the Tall Timbers Fire Ecology Conference 7:79-109.

Vogl, R. J., W. P. Armstrong, K. L. White, and K. L. Cole. 1988. The closed-cone pines and cypresses. Pages 295-358 *In* M. G. Barbour and J. Major (editors), Terrestrial Vegetation of California. Wiley, New York.

Williamson, G. B., and E. M. Black. 1981. High temperature of forests fires under pines as a selective advantage

over oaks. Nature 293:643-644.
Williamson, N. M., and J. K. Agee. 2002. Heat content variation of interior Pacific Northwest conifer foliage. International Journal of Wildland Fire 11:91-94.
Zar, J. H. 1999. Biostatistical Analysis. Prentice-Hall, Upper Saddle River, New Jersey.
Received
Accepted for Publication

Table 1. Species sampled, fire adaptive strategy, and collection sites. Resister (R) or evader (E) designations are based on information from Rowe (1983) and Agee (1993).

Common name	Latin name	Strategy	Collection site	Principal distribution
Jeffrey pine	*P. jeffreyi*	R	Tahoe Basin, CA	Sierra Nevada, Basin and Range forests
Ponderosa pine	*P. ponderosa*	R	Kyburz, CA	Sierra Nevada, Cascade, Rocky Mountain forests
Longleaf pine	*P. palustris*	R	Ocala, FL	Atlantic, Gulf coastal plain forests
South Florida slash pine	*P. elliottii* var. *densa*	R	Lake Placid, FL	South Florida sandhill, flatwood stands
Knobcone pine	*P. attenuata*	E	Gold Run, CA	Central California, southern Oregon small stands
Monterey pine	*P. radiata*	E	Point Lobos, CA	Monterey Peninsula forests
Pond pine	*P. serotina*	E	Ocala, FL	Southeastern pocosins, wettest flatwood forests
Ocala sand pine	*P. clausa* var. *clausa*	E	Ocala, FL	Central Florida scrub forests

Table 2. Means of cone weight and burning characteristics from 10 test burns for each pine species. Values in a row with identical letters are not significantly different.

	Jeffrey	Ponderosa	Longleaf	SF slash	Knobcone	Monterey	Sand	Pond
Maximum flame length (cm)	69.3	57.5 [a]	87.1	57.6 [a]	49.3 [b]	50.1 [b]	44.4 [c]	42.7 [c]
Flame time (sec)	262 [b]	250 [b]	208 [b]	207 [b]	740 [a]	605 [a]	207 [b]	328 [b]
Smolder time (sec)	4412	864 [b]	2958 [a]	2388 [a]	1262 [b]	1652 [b]	178 [c]	188 [c]
Burn time (sec)	4674	1114	3166	2595 [a]	2002 [a]	2257 [a]	385 [b]	516 [b]
Fuel combusted (%)	89.0 [a]	78.9	93.8 [a]	88.8 [a]	68.0	44.0 [b]	49.3 [b]	43.6 [b]
Weight loss (mg/sec)	19.1 [b]	24.9 [ab]	17.1 [b]	7.9	28.8 [a]	18.8 [b]	13.3	18.0 [b]
Cone weight (g)	96.6 [a]	24.2 [b]	56.1	22.2 [b]	70.0	88.1 [a]	10.3	19.8 [b]

Table 3. Means of cone weight and burning characteristics from 20 test burns per group to compare factors. Values in a row with identical letters are not significantly different.

	Western resisters	Eastern resisters	Western evaders	Eastern evaders
Maximum flame length (cm)	63.4	72.4	49.7 [a]	43.6 [a]
Flame time (sec)	256 [a]	207 [a]	672	268 [a]
Smolder time (sec)	2638 [a]	2673 [a]	1457	183
Burn time (sec)	2894 [a]	2880 [a]	2129	451
Fuel combusted (%)	91.3	84.0	56.1	46.4
Weight loss (mg/sec)	22.0 [a]	12.5 [b]	23.8 [a]	15.6 [b]
Cone weight (g)	60.4	39.2	79.1	15.0

Table 4. Means of cone weight and burning characteristics from 40 test burns per group to compare the main effects of fire adaptive strategy. Values in a row with identical letters are not significantly different.

	Resisters	Evaders
Maximum flame length (cm)	67.9	46.6
Flame time (sec)	232	470
Smolder time (sec)	2656	820
Burn time (sec)	2888	1290
Fuel combusted (%)	87.6	51.3
Weight loss (mg/sec)	17.2 [a]	19.7 [a]
Cone weight (g)	49.8 [a]	47.0 [a]

Table 5. Means of cone weight and burning characteristics from 40 test burns per group to compare the main effects of geographic region. Values in a row with identical letters are not significantly different.

	Western	Eastern
Maximum flame length (cm)	55.6 [a]	58.0 [a]
Flame time (sec)	464	238
Smolder time (sec)	2048	1428
Burn time (sec)	2512	1666
Fuel combusted (%)	70.0 [a]	68.8 [a]
Weight loss (mg/sec)	22.9	14.1
Cone weight (g)	69.7	27.1

Table 6. Means of burning characteristics from 10 test burns for needles from three eastern evaders. Values in a row with the same letter are not significantly different. Data for jack pine and sand pine are from Fonda (2001).

	Pond	Jack	Sand
Maximum flame length (cm)	87.2	46.4	50.3
Flame time (sec)	89.1	167.8	195.4
Ember time (sec)	213.2	69.9	124.6
Burn time (sec)	302.3 [a]	237.6	319.9 [a]
Fuel combusted (%)	88.5	60.7 [a]	61.6 [a]
Mean rate of weight loss (mg/sec)	45.6 [a]	39.3 [a]	29.1

Figure captions *(figures not included here)*

Figure 1. Cones of pond pine, a fire evader, scattered in the stand.

Figure 2. Cones of Jeffrey pine, a fire resister, around tree bases.

Figure 3. Cones of species used in this study. Front row, from left: ponderosa pine, south Florida slash pine, pond pine, sand pine. Back row, from left: Jeffrey pine, longleaf pine, Monterey pine, knobcone pine.

Figure 4. Interactions between fire adaptive strategy and geographic region, based on the data in Table 3. All interactions were significant, except weight loss rate. W,R: western resisters; W,E: western evaders; E,R: eastern resisters; E,E: eastern evaders.

APPENDIX H. PROGRESS REPORTS

2001 – Full Study Plan submitted – only the schedule submitted here.

SCHEDULE - This study begins September 2001 and ends December 2004 (3 years) – amended to end Aug., 2005

2001:

1. Literature Review, October 2001 [UF/TNC]
2. Site selection, December 2001[ALL]

2002:

3. Detailed study plan, February 2002 [ALL]
4. Pre-treatment field data collection on both permanent (EAFB) and supplemental sites. Data collected at EAFB: 50 trees with pins, 15 subplots within treatments, soil/duff samples, Brown transects, 50 supplemental trees. Data collected at supplemental sites: duff reduction, duff samples, Brown transects, January-February 2002 [PNW/UF]
5. Duff moisture collections and model creation; weather station data collection, January 2002-December 2003 [EAFB]
6. Treatment application and day-of-burn weather, fire behavior, and duff data, February 2002-May 2002 [EAFB/PNW/UF]
7. Post-treatment data collection: consumption sampling, individual tree measures (ht, cht, dbh, bark thickness, char ht, % scorch, physiological measures, tree cores), soil/duff sampling, Brown transects, March 2002-May 2003 [UF/EAFB/PNW/JEC]
8. Individual tree experimentation & duff composition/structure (Ordway Preserve), June – August – December 2002 [UF]
9. Mortality Assessment, August 2002 [UF]
10. Develop fuel bed characteristics of sites (for Consume inputs). September 2002 [PNW]
11. Progress Report detailing consumption results and prescription windows, duff moisture model, October 2002 [ALL]

2003:

12. Consume 3.0 release, users manual, and training, January 2003 [PNW]
13. Supplemental site burns, data collection, & analysis, January – April 2003 [ALL]
14. Mortality assessment, September 2003 [UF]
15. Fuel consumption manuscript, September 2003 [PNW]
16. Develop web-site and initiate field tours of the study sites, September 2003 [EAFB]
17. Progress report & initial mortality findings, October 2003 [ALL]
18. Publish results in outreach newsletters, October 2003 [ALL]

2004:

19. Consumption Validation Burns (Moody Tract and elsewhere), February 2003 [ALL]
20. Final mortality assessment, August 2004 [UF]
21. Develop free prescription guideline publication for burning duff, September 2004 [PNW]
22. Manuscript on tree stress & mortality of trees subjected to duff consumption, December 2004 [UF]
23. Final report on duff consumption, tree mortality, and mechanistic evaluation December 2004 [ALL]

2002

Project title: Duff Consumption and Southern Pine Mortality

Principal Investigators:
J. Kevin Hiers, Eglin Air Force Base, Natural Resource Branch, 107 N. Highway 85, Niceville, FL 32578
Dale Wade, USDA Forest Service, Southern Research Station, 320 Green Street, Athens, GA 30602
Dr. Doria Gordon, The Nature Conservancy and University of Florida, Box 118526, Gainesville, FL 32611-8526
Dr. Robert J. Mitchell, Joseph W. Jones Ecological Research Center, Rt. 1 Box 2324, Newton, GA 31770
Co-investigators:
Roger D. Ottmar, Sue Ferguson, and *Robert E. Vihnanek*, Seattle Forestry Sciences Laboratory, 4043 Roosevelt Way N.E., Seattle, WA 98105
J. Morgan Varner, University of Florida, Box 118526, Gainesville, FL 32611-8526
Contact information (phone, e-mail): hiersjk@eglin.af.mil phone (850) 882-6232 x309 fax (850) 882-5321

Description of project: To determine threshold moisture conditions that initiate and maintain smoldering combustion within the forest floor of long-unburned longleaf pine stands and to document the consequences of this combustion for overstory pine mortality. The project will also develop prescription parameters and planning tools for managers to burn these stands while minimizing overstory pine mortality.

Status report: This project is on schedule and within budget.

Project began with extensive review of literature related to longleaf pine mortality, fire effects, and forest floor accumulation and fuel properties, which has been submitted as the first deliverable (see Appendix 1). Early work also focused on discussions with land managers from AL, FL, GA, and MS. Study design and implementation meetings were held between cooperators in Nov. 2001. Site visits followed, with selection of 3 sites at Eglin Air Force Base, FL, with 4 treatment blocks in each: dry burn, moist burn, wet burn, and the no-burn control. Meteorological stations were installed at all three sites to collect data on: fuel stick temperature, air temperature, soil temperature (at 3 cm), daily & 15-min. precipitation, relative humidity, fuel stick moisture, duff moisture (upper, mid, and lower), and wind direction. Real-time data have been available to collaborators and the public on the PNW website (http://www.fs.fed.us/pnw/fera/nfp/pnw4/eglinframeset.html).

Within each treatment block, we characterized the stands and their fuels before and after fire. Characters measured were: (1) pre-burn volumetric duff moisture; (2) site woody fuel loading (Brown transects); (3) forest floor depth and material type; (4) large woody fuels (wired logs); (5) forest floor bulk density; (6) crown cover; (7) shrub cover; (8) and photographs of stand conditions. Within all treatment replicates, herbaceous and grass fuels were sampled on 20 subplots before and after a burn using a semi-random plot design, clipping, and weighing. Pre- and post-burn shrub biomass has been calculated by clipping and weighing of fuel samples. To characterize forest stands, we measured 100 randomly selected trees per block for total height, height to live crown, DBH, and noted signs of damage (basal scars). To track physiological condition of treated trees, we sampled fine root, coarse root, and stem non-structural carbohydrates of trees with low, moderate, and severe duff consumption (immediately following burning, so values could be used as pre-burn values). Post-fire variables measured at each site were: (1) duff consumption; (2) char heights; (3) scorch height; (4) percent of canopy volume scorched; (5) canopy consumption; (6) stem damage; and (7) woody consumption. All consumption samples have been dried, processed, and data have been entered. Data analysis will continue, with summary consumption results expected by December.

All 9 treatment burns were completed on all experimental sites (3 dry, 3 moist, 3 wet) during February, March, and April 2002 as scheduled. To avoid confounding burn severity with duff moisture condition on the day of burn, we standardized burn severity through modification of firing pattern with modest success (table 1).

We also initiated an intensive deep raking (to mineral soil) and stem girdling experiment on 40 trees in 09/02. These trees will be followed seasonally for mortality and annually for radial growth. These results will aid our understanding of pine response to cambial heating (=girdling), duff smoldering (=deep raking), and the combination (=raking and girdling).

Table 1. Summary of fire treatments and burn results (means and S.D.) for 9 burns at Eglin AFB, FL in 2002

Stand	Burn Treatment		Scorch Ht.(m)	Scorch Vol.(%)	Char Ht. (m)	Consumption (%)
Ramer T S	wet	(03/05/02)	8.1 (2.0)	5.8 (11.3)	1.4 (0.8)	7.7 (15.1)
Ramer T N	moist	(02/22/02)	10.8 (2.6)	8.8 (15.4)	1.0 (0.8)	21.9 (20.5)
Ramer T M	dry	(03/24/02)	12.3 (2.9)	34.3 (36.6)	2.8 (1.6)	52.1 (30.9)
RC Xeric NE	wet	(03/14/02)	8.0 (1.7)	4.3 (5.2)	0.9 (0.6)	33.6 (32.5)
RC Xeric NW	moist	(03/08/02)	11.4 (3.2)	35.9 (32.7)	3.1 (1.5)	63.4 (31.5)
RC Xeric SE	dry	(04/07/02)	12.1 (2.6)	58.4 (31.4)	3.2 (1.4)	84.4 (20.4)
RC Mesic SE	wet	(03/04/02)	13.1 (3.3)	23.6 (26.7)	2.1 (1.4)	34.4 (22.0)
RC Mesic Mid	moist	(02/22/02)	16.7 (3.4)	71.7 (29.7)	5.1 (2.8)	45.1 (24.8)
RC Mesic SW	dry	(04/24/02)	15.3 (3.7)	70.4 (33.7)	4.1 (2.2)	73.2 (28.3)

Outputs: Since project commencement, we have:
1 **talk** and **abstract** at Society for Ecological Restoration Coastal Plain Conference (02/02; FL),
1 Site **tour** for 16 participants at Society for Ecological Restoration Coastal Plain Conference (02/02; FL),
1 Field **tour** for 90 Florida Division of Forestry personnel (04/02; FL),
2 **Abstracts** accepted for Longleaf Alliance Regional Conference (09/02; NC),
Invited for **Panel discussion** on USDA-FS Fire Science and Fire Management Workshop (11/02; FL),
1 **Paper** delivered at the NIFC Science Workshop (01/02),
1 **Symposium abstract** accepted for Ecological Society of America (09/02; GA),
1 **invited talk** at Duke University, Nicholas School of the Environment (11/02),
1 **Web page** developed for fire & stand weather results (http://www.fs.fed.us/pnw/fera/nfp/pnw4/eglinframeset.html)
1 **Web page** promulgating the results of duff moisture and weather (http://flame.fl-dof.com/Env/RX/ruthford.pdf)
1 **Manuscript** on longleaf pine mortality being readied for review with final manuscript to be completed 12/02

Issues/concerns affecting the project: During year 2, availability of supplemental sites that are easy to burn may be an issue. We are addressing this now by "over-scheduling" burns (arranging 6 sites, expecting to burn 3). Additional sites will be used as validation sites described in year three.

Preliminary data and discussions with cooperators and land managers suggest more work is needed in characterizing pine forest floor, particularly fuel characteristics (ignition, extinction of components [litter, bark, cones, leaves]). We are attempting to address these concerns in the intensive, single-tree portion of the study and in lab experimentation.

2003

Project title: Duff Consumption and Southern Pine Mortality

Principal Investigators:
J. Kevin Hiers, Eglin Air Force Base, Natural Resource Branch, 107 N. Highway 85, Niceville, FL 32578
Dr. Joseph J. O'Brien (for Dale Wade), USDA Forest Service, Southern Research Station, 320 Green Street, Athens, GA 30602
Dr. Doria Gordon, The Nature Conservancy and University of Florida, Box 118526, Gainesville, FL 32611-8526
Dr. Robert J. Mitchell, Joseph W. Jones Ecological Research Center, Rt. 1 Box 2324, Newton, GA 31770

Co-investigators:
Roger D. Ottmar, Sue Ferguson, and *Robert E. Vihnanek*, Northwest (PNW) Research Station, Pacific Wildland Fire Sciences Laboratory, 400 N. 34th Street, Suite 201, Seattle, WA 98103
J. Morgan Varner, University of Florida, Box 118526, Gainesville, FL 32611-8526

Contact information: hiersjk@eglin.af.mil phone (850) 882-6232 x309 fax (850) 882-5321

Description of project: To determine threshold moisture conditions that initiate and maintain smoldering combustion within the forest floor of long-unburned longleaf pine stands and to document the consequences of this combustion for overstory pine mortality. The project will also develop prescription parameters and planning tools for managers to burn these stands while minimizing overstory pine mortality.

Status report: This project is on schedule and within budget.

Three supplemental burns were conducted in 2003 at Ft. Gordon, GA, Baxley, GA, and Gainesville, GA. These burns successfully demonstrated our progress to a variety of managers and provided additional consumption measures to enhance regression analyses. The primary focus of the research team over the past year has been data management and statistical analysis. Consumption data within all treatment burns (2002) and supplemental burns (2003) have been measured, entered, and reduced. Statistical analyses of consumption measures within the block design are on going. Consumption data from these burns have been used in the validation of predictions made within Consume 3.0, as specified in the study plan. The first year post-burn mortality surveys have been completed in all treatment blocks. Results indicate significant mortality in dry burns where consumption was greatest (Figure 1). Two year post-burn observations from sampling in previously funded study plots burned in 2001 indicate more mortality can be expected. Thorough analysis of the weather data for developing prescription parameters is on going, but preliminary results are presented in Figure 2.

Weather stations were set up in 2002 to monitor conditions at the Ramer Tower site. One of these stations was left in place to monitor the 2002 burns and as of August 2003 is still collecting data. Two weather stations were set up at the other treatment locations in January of 2002 and collected data until May 2003. All weather stations measured air temperature, relative humidity, wind speed, wind direction, 10-hour fuel temperature, 10-hour fuel moisture, barometric pressure, and precipitation. Sensors at all stations had a sampling interval of 10 seconds and logged data averages every 15 minutes. Forest floor moisture was monitored at all stations using Campbell Scientific model CS-615 time-domain reflectometer (TDR) probes. All weather stations sampled and logged the raw period output from the CS-615 probes. We refer to this uncalibrated output as the moisture index (MI). Three moisture probes were inserted horizontally into the forest floor organic layer at each station, at varying depths. Litter (needles and bark slough with no evidence of decay) and duff (decomposing organic material) layers were highly variable across the landscape, with shallow layers (1-5 cm litter, 1-5 cm duff) in open areas and significantly thicker layers (5-10 cm litter, 5-10 cm duff) surrounding the base of most large longleaf pine trees. In all locations, the underlying mineral soil was well-drained sand.

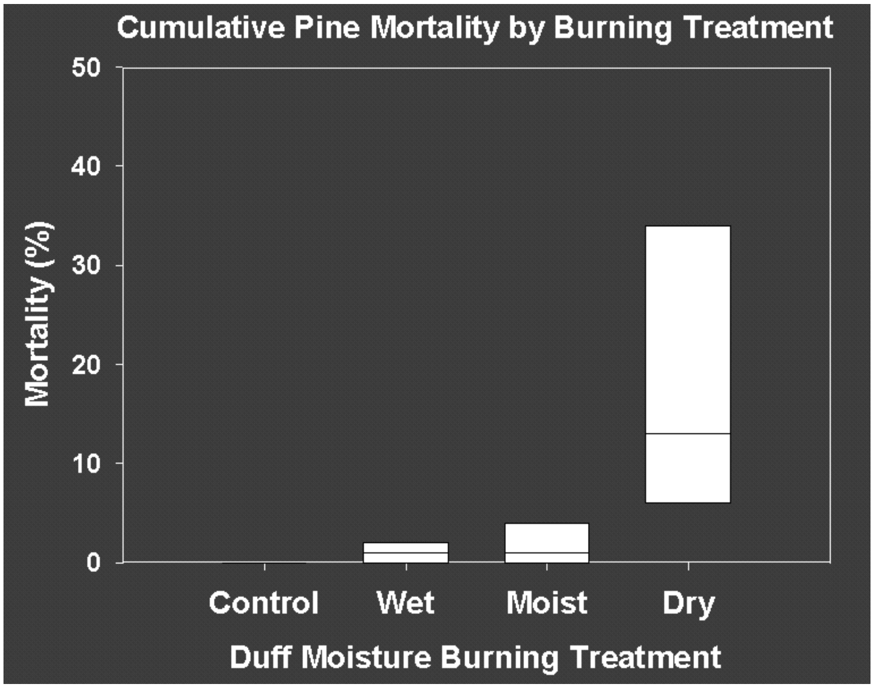


Figure 1. Percent overstory mortality within 13 treatment burns under varying duff moisture conditions and unburned controls; delayed mortality from previous JFSP study suggests that mortality will increase in the second year since treatment burns.

Analysis of the relationship between the duff layer moisture index and wind, relative humidity, temperature and precipitation found that a relatively simple model could explain nearly all of the variability in the moisture index. 1300 LST values were used to filter out the diurnal cycle and to create a model consistent with the National Fire Danger Rating System, which uses 1300 LST observations to calculate its indexes. Many predictors, including past 24-hour average relative humidity, past 24-hour average 10-hour fuel moisture, past 24-hour precipitation duration, and past 48-hour precipitation were tested in multiple linear regressions. It was found that the three predictors yielded the highest r^2 and correlation values for a prediction of the duff layer moisture. A multiple linear regression of the duff moisture index with the previous day's duff moisture index, the square root of the past 24 hour precipitation, and the square root of the precipitation from the previous 24 hour period yields an r^2 value of 0.9997 and a correlation value of 0.95. Some predictors, such as past 24-hour precipitation duration, also fit quite well, but the correlation values were not as high as for the total past 24-hour precipitation amount.

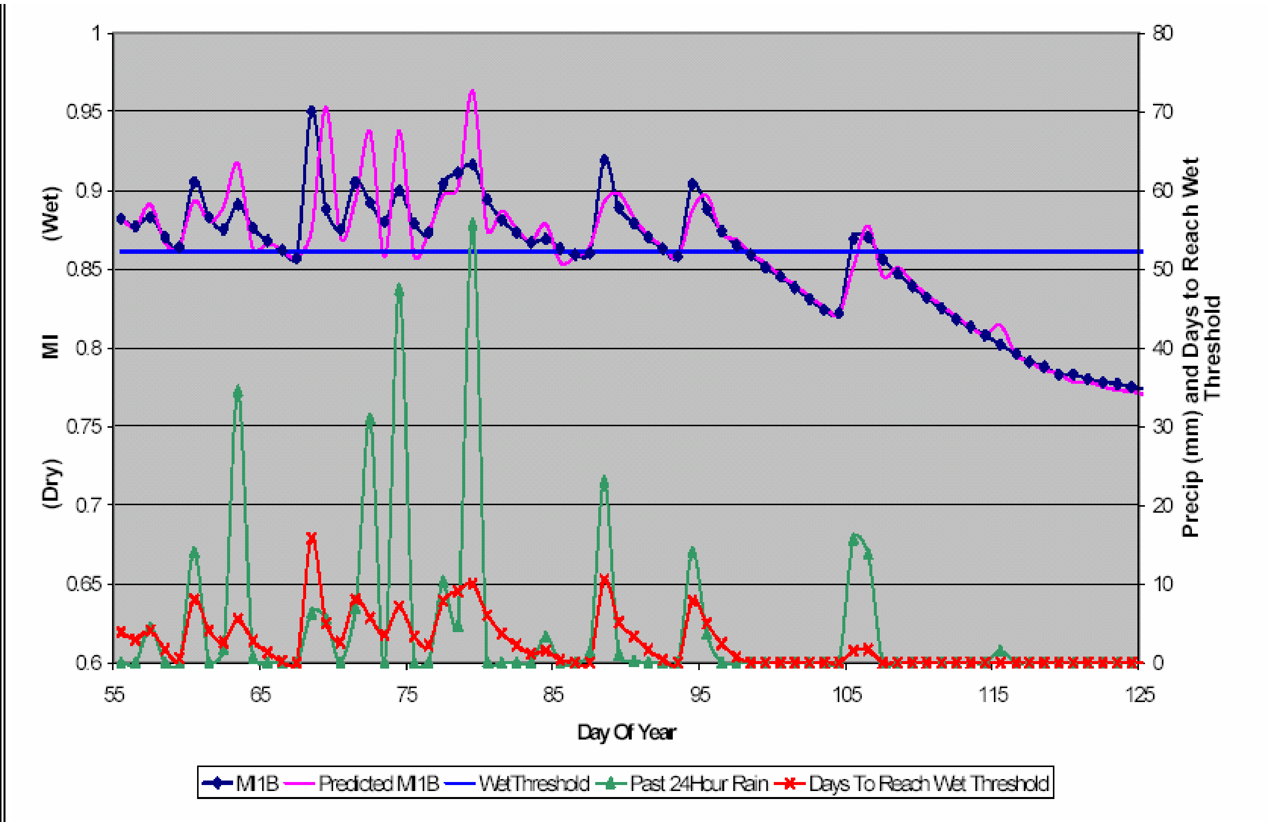


Figure 2. Predictive model of duff moisture (Top solid line) and variables selected in the multiple regression. Solid line at MI value of 0.86 represents the safe (moist) burning conditions under which the least duff consumption was observed.

A simple model developed from a multiple linear regression of past moisture index and past precipitation can provide a useful tool for predicting the evolution of future moisture conditions. By using a long time series of continuous data in 2001 to derive the equation, correlation values remain high when tested against data in 2002 and 2003. Real-time data have been available to collaborators and the public on the PNW website: (http://www.fs.fed.us/pnw/airfire/fm/eglin). The PNW research station is in the process of developing a duff moisture calculator on this website to facilitate the determination of safe burning conditions.

We have completed sampling 1-year post burn for non-structural carbohydrate in all treatment blocks. This will provide stand level measure of forest health via carbon status of trees in the units. Samples have been extracted at the Jones Ecological Research Center and are being analyzed.

In September 2003, we began the intensive individual tree burning to determine proximal causes of duff burning-related pine mortality. In this study we are attempting to isolate causes of mortality (cambial damage, root damage, or combinations) in a mature, long-unburned (36 yrs) longleaf pine stand at the Ordway Preserve near Gainesville, FL. Treatment pines are instrumented with thermocouples to monitor during and post-fire temperatures along the bark, within duff, and at 5, 10, and 20 cm beneath the mineral soil surface. Response variables for this portion of the study will include non-structural carbohydrate change, radial growth, and mortality. These results will aid our understanding of pine response to cambial heating, duff smoldering, and the combination of these stressors.

Outputs: Since Last Year's Progress Report, we have:

1 **Symposium Talk** and **Abstract** at Ecological Society of America Annual Meeting (08/03; GA),

2 **Abstracts** accepted for 2nd International Fire Congress Regional Conference (09/03; FL),

1 **Symposium** extended abstract published in proceeding for Fire and Forest Meteorology Conference, (08/03, FL),

1 **invited talk** at NW Florida Prescribed Fire Council (10/03; FL),

3 **Web pages:** one automatically displays real-time fire & stand weather results http://www.fs.fed.us/pnw/airfire/fm/eglin/, one describes a related National Fire Plan project http://www.fs.fed.us/pnw/fera/nfp/combustion/index.html, and one presents the first year results from a briefing at the NW Florida Prescribed Fire Council http://flame.fl-dof.com/Env/RX/councils/north/,

1 **Manuscript** on the problems and phenomena of duff burning and weather to be submitted 11/03,

1 **Manuscript** on longleaf pine mortality being readied for review with final manuscript to be completed 12/03,

1 **Extended Abstract** published in the Proceedings of the 4th Longleaf Alliance Meeting, Southern Pines, NC (07/03),

2 **Newsletter Features** in Society for Ecological Restoration Coastal Plain Chapter (Fall 03) and the Georgia Chapter of The Nature Conservancy annual newsletter,

3 **Demonstration** burns and field tours at supplemental sites in Augusta, GA, Baxley, GA, and Gainesville, FL,

1 **Invited Feature** in the Longleaf Alliance Outreach Newsletter (11/03; AL).

Issues/concerns affecting the project: For ease of logistics during year 3, validation burns will be selected at the same sites used for supplemental burns in year two, applying fire to new areas at those sites. The individual tree manipulations of fine root mortality and cambium damage are still occurring at the Ordway Preserve in Gainesville, FL, and final mortality counts for these manipulations may not be known for up to two years. This dramatic delay in mortality has delayed publishing of the first consumption manuscript from year 1 burns, as dying trees are still appearing in the stands.

Preliminary data suggests that the duff moisture probes used in conjunction with the weather stations on study site burns is an excellent tool for predicting safe duff moisture conditions. While analyses are still being performed to address predictive models without using duff probes, this finding points to the need for adding moisture probes to regional RAWS stations for use by managers.

2004

J. Kevin Hiers, Dale Wade, Doria Gordon, Morgan Varner, Robert Mitchell, and Roger Ottmar
Eglin Air Force Base, Natural Resource Branch,
107 N. Highway 85, Niceville, FL 32578

Location: Eglin Air Force Base, Walton, Okaloosa, and Santa Rosa Counties and several other sites in Florida and Georgia

Duration: 2001–2004

Objective: Determine threshold moisture conditions that initiate and maintain smoldering combustion within the forest floor of longleaf pine stands and document the consequences of this combustion for overstory tree mortality. Develop prescription guidelines for burning these stands that utilize this information to minimize overstory mortality. Describe stand structure and composition of long-unburned longleaf pine stands and the impacts of prescribed fire on these stands, including foliar and root dynamics. Additionally, examine the mechanistic relationship between duff consumption and pine mortality.

Methods: The primary experimental work was set-up at Eglin AFB in 2001-2. Four treatments were established in each of three blocks: unburned, burned when organic material on the forest floor was wet, burned when that material was moist, and burned when it was dry. Within each plot, 100 overstory visually healthy longleaf pines were pre-selected to monitor for duff consumption, root mortality following fire, and overall response to fire. Tree height, height to live crown, stem diameter, basal bark thickness, scorch height, basal organic matter loss, stored carbon in roots, and other measures are monitored in burned and unburned trees. Immediate and indirect causes of tree mortality will be evaluated. In winter 2003, three burns were conducted at other sites in Florida and Georgia. Duff height around up to 100 trees was measured before and after fire, duff moisture was measured on the day of the fire, and the same post-burn data were collected. In all sites trees continue to be monitored for stress and mortality. We have completed sampling 1-year post burn for non-structural carbohydrate in all treatment blocks. This will provide stand level measure of forest health via carbon status of trees in the units.

In a separate study, more specific characteristics of fuels and smoldering are being assessed. Mechanistic evaluation of sources of mortality is under investigation using a factorial approach that combines stem damage (girdle using fire or no damage) with root damage (duff raking or none) with canopy scorch (scorched or not). In 2004, we will determine prescriptions using our understanding of the fuel characteristics and tree responses. Tree responses in sites that incorporate these prescriptions into fire application with then be determined.

Progress/Results: Prescribed burning of the sites at Eglin AFB was completed in spring 2002. Trees were marked and data collection continues. The organic layers around long-unburned longleaf pine trees have been characterized, and their combustion properties investigated. Pre- and post-burn data have been collected for the three prescribed fires conducted in early 2003. The results indicate significantly higher tree mortality in low moisture burns where soil consumption was greatest. Two year post-burn observations from sampling in previously funded study plots burned in 2001 indicate more mortality can be expected.

Analysis of the relationship between the duff layer moisture index and wind, relative humidity, temperature and precipitation found that a relatively simple model could explain nearly all of the variability in the duff moisture index: the previous day's duff moisture index, the square root of the past 24 hour precipitation, and the square root of the precipitation from the previous 24 hour period yields an r^2 value of 0.9997 and a correlation value of 0.95. Consumption data from the burns have been used in the validation of predictions made within Consume 3.0, an organic soil model to be used in conjunction with the existing fuel model for prescribed fire.